U. S. DEPARTMENT OF AGRICULTURE.
BUREAU OF PLANT INDUSTRY—BULLETIN NO. 216.
B. T. GALLOWAY, *Chief of Bureau.*

THE RUSTS OF GRAINS IN THE UNITED STATES.

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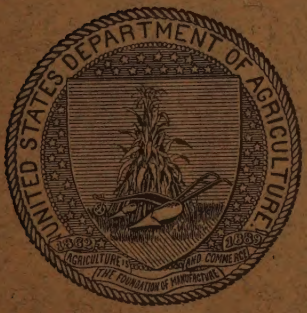
22 MAY 1945

BY
E. M. FREEMAN, *Collaborator,*
AND
EDWARD C. JOHNSON,
Pathologist in Charge of Cereal Disease Work, Office of Grain Investigations.
In Cooperation with the Minnesota Agricultural Experiment Station.

ISSUED AUGUST 15, 1911.



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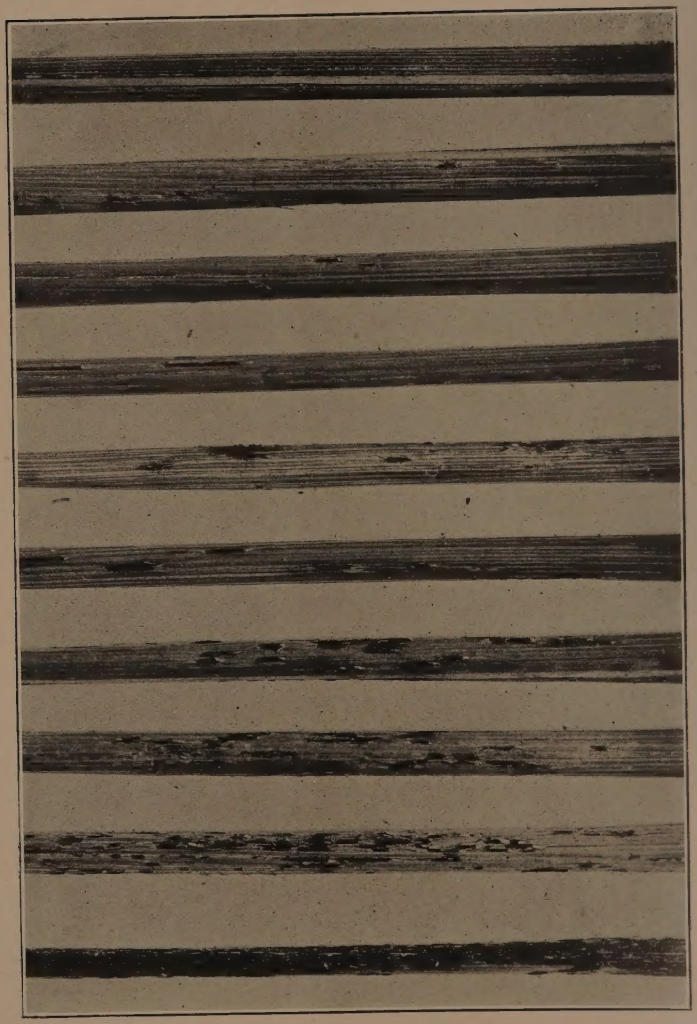

STEM RUST OF WHEAT ON WHEAT CULMS, SHOWING VARIOUS DEGREES OF ATTACK.

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., March 25, 1911.

Sir: I have the honor to transmit herewith a technical paper entitled "The Rusts of Grains in the United States," by E. M. Freeman, Collaborator, and Edward C. Johnson, Pathologist in Charge of Cereal Disease Work. This paper embodies the results of recent research by the Office of Grain Investigations in cooperation with the Minnesota Agricultural Experiment Station into the distribution, relationships, physiology, and life history of the important grain rusts, and gives much new information on the "biologic forms" of rusts, vitality of successive uredo generations, wintering of the uredo generation, and climatology in relation to rust epidemics. Former experiments on rust prevention are summarized and methods of selection and breeding of grains for rust resistance indicated.

The grain rusts continue to be of large economic importance, and as this paper is another step advancing our knowledge concerning them I recommend that it be published as Bulletin No. 216 of the series of this Bureau.

Respectfully,

Wm. A. Taylor,
Acting Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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THE RUSTS OF GRAINS IN THE UNITED STATES.

INTRODUCTION.

That rusts are among the most serious diseases of grains in the United States is generally granted. As they are always present in humid grain-growing districts to a greater or less extent, it is almost impossible to make accurate estimates of the damage caused by them. Estimates are, perhaps, more often too low than too high, so that the losses of fifteen to twenty million dollars annually, estimated by Bolley (28,[1] p. 615) for the United States, certainly seem within reason. Numerous references to losses from rust epidemics in different countries may be found.

The most severe epidemic in the last decade occurred in the United States in 1904. It was particularly prevalent in the spring-wheat belt of the northern Mississippi Valley, where the three States, Minnesota, South Dakota, and North Dakota, in which the bulk of the hard spring wheat of the United States is raised, suffered perhaps more than any other section of the country. Table I shows a comparison of the wheat crop in these three States for the years 1903, 1904, and 1905, affording a basis for an estimate of the losses sustained in this epidemic.

TABLE I.—*Wheat crop in Minnesota, South Dakota, and North Dakota in 1903, 1904, and 1905.**

Year.	Acreage.	Yield per acre.	Total yield.
		Bushels.	*Bushels.*
1903	13,167,110	13.15	173,146,171
1904	13,193,695	11.65	153,793,233
1905	14,069,251	13.66	192,190,759

* Compiled from U. S. Crop Report.

Average yield per acre for 1903 and 1905=13.4 bushels; for 1904=11.65 bushels. Reduction in yield per acre in 1904 below the average for 1903 and 1905=1.75 bushels. Total reduction in yield in 1904=13,193,695 (acres)×1.75=23,088,966 (bushels). Average price for the three States for 1903 and 1905=66.8 cents. Reduction in value in 1904 below the average for 1903 and 1905=23,088,966×66.8 cents=$15,423,429.28.

[1] The serial numbers in parentheses throughout this bulletin refer to the titles in the "Bibliography" on pages 79–82.

An average reduction in yield of 1.75 bushels per acre in 1904 as compared with the preceding and following years gives a total reduction of over 23,000,000 bushels, valued at more than $15,000,000.[1] The greater part of this reduction in yield and consequent loss was undoubtedly due to rust. It is exceedingly conservative to put the loss in these three States in 1904 as high as $10,000,000; and when we consider the additional losses in the other wheat-growing districts of the United States the aggregate is enormous.

KINDS OF RUSTS IN THE UNITED STATES.

This paper deals only with the rusts of the small-grain crops, wheat, barley, rye, and oats, and includes the following forms:[2]

Puccinia graminis Pers. on wheat, rye, oats, and barley, commonly known by the misleading term "black rust," but more appropriately known as "stem rust," as it generally is confined more or less closely to the stem and sheath (Pl. I).

P. rubigo-vera tritici[3] on wheat, known as "orange leaf rust," or "leaf rust of wheat."

P. rubigo-vera secalis[3] on rye, known as "orange leaf rust," or "leaf rust of rye."

P. coronata Corda. on oats, known as "leaf or crown rust of oats."

P. simplex (Körn.) Erikss. and Henn. on barley, known as "leaf rust of barley."

These rusts, in common parlance, are classed as stem or leaf rusts, a convenient grouping which directs attention to the chief though not exclusive location of the rust on the host plant.

DISTRIBUTION OF RUSTS IN THE UNITED STATES.

GENERAL STATEMENT.

All of the grain rusts, with the possible exception of stem rust of rye and the leaf rust of barley, are found throughout the United States wherever their host cereals are grown. As to the distributon of the barley leaf rust, less is known, because it may have been but recently introduced into this country and appears, as a rule, late in the season. It has been reported from California, Virginia, Minnesota, and Iowa and is probably of wide distribution.

Although the rusts are for the most part practically coextensive with the hosts, they are not serious in all localities. Epidemics may occur in almost any grain-growing region, but they occur less frequently in some sections than in others. In general, the area most affected is the valley of the Mississippi and its tributaries, comprising the region west of the Alleghanies and east of the ninety-eighth

[1] Even comparing the yield, 11.65 bushels per acre, with the 10-year average (12.2 bushels per acre) for the three States from 1896 to 1905 (obtained by computing the averages in the three States), there was a reduction in yield in 1904 of more than 0.5 bushel to the acre.

[2] A few other rusts have been reported, some perhaps by mistake and some of such rare occurrence as to be of no economic importance. *Puccinia glumarum* (Schm.) Erikss. and Henn., the yellow rust of wheat, which is a very common and serious rust in Europe and India, has not yet appeared in this country.

[3] The trinomial terminology for these two rusts was first used by Carleton (30, p. 10).

meridian, which marks the eastern border of the semiarid lands of the central United States. It thus includes a large portion of the great grain-growing districts of this country. The rusts are also very severe and of annual occurrence in the small, isolated districts on the west side of the Coast Range in California, in eastern and southern Texas, and in parts of the Atlantic Coast States. They are an important factor in the grain-growing regions of eastern Washington and Oregon. In general, where the annual rainfall is 20 inches or more, rust may be a serious menace to crops. In areas where the annual rainfall is less than 20 inches rusts are generally of little importance. Such dry areas occur in the United States just east of the Rocky Mountains, extending eastward to the ninety-eighth meridian and in the intermountain areas, including Wyoming, much of Montana, Idaho, Utah, Colorado, New Mexico, southeastern Oregon, and the interior valleys of California. Here in most years rusts are comparatively rare, though in the great rust epidemic of 1904 some of these areas, including California, were affected.

AREAS MOST LIABLE TO RUST.

The area where rust is particularly a menace is the hard spring-wheat belt of Minnesota, North Dakota, and South Dakota. The States bordering the Ohio River Valley, including Kentucky, Illinois, Indiana, and Ohio likewise are frequently attacked by rust. In the Southern States of the eastern half of the United States—that is, south of and including Tennessee and North Carolina—rust of certain cereals has been so serious as almost to prohibit the growing of them in those regions. It is very difficult, for instance, to grow spring oats profitably in portions of the southernmost tier of States east of the Mississippi River, one of the chief difficulties being rust. Almost nowhere in this southeastern part of the United States are the small grains, with the exception of winter oats, grown at all extensively.

DISTRIBUTION OF THE DIFFERENT RUST SPECIES.

Stem rust of wheat.—The stem rust of wheat (*Puccinia graminis tritici* Erikss. and Henn.) is of great importance in the hard winter and hard spring wheat belts of the Great Plains area and in the States bordering the Ohio River. In Maryland, Virginia, and other Eastern States it has been almost entirely absent for many years, but is by no means unknown. In Washington and Oregon it is frequent and virulent. In the interior mountain valleys, between the Rocky Mountains and the Sierra Nevada Mountains, and in the nonirrigated western area of the Great Plains, it is only occasionally found and is seldom serious. In the interior valleys of California it is occasionally epidemic, though usually of slight importance. On the coast of California

it is always present and almost always virulent. Little grain is grown in this region. In the Southern States only a small quantity of wheat is grown, and here this rust is often severe. In the southern half of Texas it makes wheat growing a hazardous undertaking. Even in northern Texas it is a factor of great importance. The greatest rust epidemic of the last decade, which was due to the stem rust of wheat, occurred in 1904 and extended over the entire Mississippi Valley and up into the wheat fields of the Canadian Northwest, being particularly severe in the spring-wheat belt. It invaded the dry lands west of the Rocky Mountains and was severe in the interior valleys of California. A serious attack of stem rust of wheat was also experienced in the spring-wheat belt in 1902 and in 1905.

Leaf rust of wheat.—The occurrence of leaf rust (*Puccinia rubigo-vera tritici* Carleton) is also coextensive with wheat culture. It is more common in many districts than stem rust. In the whole eastern half of the United States it is present every year, usually to a considerable extent. Visitations amounting to epidemics are not infrequent, but the losses caused are not comparable to those of the stem-rust epidemic and are disregarded by the ordinary farmer, who accepts them as inevitable. In the Atlantic States the leaf rust is the chief rust of wheat and is very severe in some seasons. Like the stem rust, it follows more or less closely the rainfall lines, being of little importance in the arid sections of the country. In the Palouse district of Washington, Idaho, and Oregon, however, it is usually abundant.

Stem and leaf (or crown) rusts of oats.—The presence of stem and leaf rusts of oats (*Puccinia graminis avenae* Erikss. and Henn., and *Puccinia coronata* Corda) is coextensive with the culture of that grain. The stem rust of oats, if not more harmful, is fully as destructive as the stem rust of wheat, and its distribution is somewhat similar. It is almost invariably accompanied by the leaf rust (*Puccinia coronata*), which is probably the most destructive of the leaf-rust group.

Attention should be called to the fact that the stem rust of oats is not nearly so closely confined to the stem as is that of wheat, but is very frequently found on the leaf blades. The leaf and stem rusts of oats are usually commingled, and it is difficult to determine how much of the resulting damage is due to each. The leaf rust, however, is seldom found on the spikelets or the spikelet stems. It is here that much of the real damage is done by the stem rust. These rusts are found extensively only east of the dry belt of the Great Plains region, with the possible exception of eastern Oregon and Washington. In the Gulf Coast States, except northern Texas, and in Georgia and South Carolina they are paramount in importance and almost prohibitive of spring-oat growing, though winter oats are quite extensively grown. Proceeding northward, the rusts continue to be of great importance.

Even as far north as Wisconsin regions are known where oat growing has been discontinued on account of rust, and epidemics have been known to extend to the Canadian line and even beyond. Two features of an oat-rust epidemic explain instances of successful crops which often occur in the midst of an epidemic. They are (1) the great variation in time of ripening of different varieties of oats, amounting to as much as three weeks or a month in some latitudes, and (2) the apparent suddenness of the appearance of the epidemic. Frequently a variety one week later than another will be ruined by rust, while the earlier variety will escape entirely. This results in the presence every year of considerable rust, amounting to a severe attack in some localities and on some varieties, while other localities and varieties escape.

Stem rust of barley.—The occurrence of stem rust of barley (*Puccinia graminis hordei*)[1] is practically coextensive with the culture of that grain, but its presence is not often a serious menace. In general, the early date of maturing of barley seems to assist this crop in avoiding injury. Barleys planted very late—for instance, those planted for fodder—are sometimes seriously attacked, while the grain barleys usually escape damage. It may be noticed, however, that this rust, like the stem rust of oats, is not so nearly confined to the stem as the wheat stem rust, but is often abundantly present on the leaves. The rust assumes more serious proportions in the Southern States. In the Great Plains area and in the dry intermountain districts it is comparatively rare.

Leaf rust of barley.—Leaf rust of barley (*Puccinia simplex* (Körn.) Erikss. and Henn.) seems to be of recent introduction. It was reported from Iowa in 1896, from California in 1905, from Minnesota in 1905, 1906, 1907, and 1908, and occurred in Virginia in 1906 in a considerable degree. In 1910 it was abundant at Laurel, Md., and also occurred in Virginia. The most abundant outbreak was in Virginia, in 1906, where the plants were well covered with rust. In Minnesota it seems to appear late in the season and has had no injurious effect on the crop. It may be classed as one of the least conspicuous of the grain rusts in point of economic importance.

Stem rust of rye.—The stem rust of rye (*Puccinia graminis secalis* Erikss. and Henn.) is fairly common, but causes little injury. The explanation of this probably lies in the fact that winter rye is grown almost exclusively in the United States, and the stem rust appears at so late a date as to cause no appreciable damage. It was fairly common in Minnesota in 1906–1908 in experimental plats on spring rye, and in 1909 was abundant. As these were light rust years as

[1] As shown later, the physiological specialization of this rust in the United States is sufficiently different from that of the stem rust on wheat to make a distinction in the name desirable, and the trinomial terminology, as here applied, is used throughout this paper.

regards stem rust, no conclusions are possible from them as to the possibility of epidemic visitation on spring rye. Bolley, at Fargo, N. Dak., during the summer of 1907, had experimental plats of winter rye in the vicinity of barberry bushes which were infected with stem rust, and these winter-rye plats were badly rusted. The rust also appeared spontaneously on greenhouse material at Washington, D. C., in 1906. The exact limits of the stem rust are not determinable on account of the meager reports, but it is safe to say that the rust at present is of very little economic importance. On the other hand, it seems probable that it is widely distributed in small quantities.

Leaf rust of rye.—The occurrence of the leaf rust of rye (*Puccinia rubigo-vera secalis* Carleton) is coextensive with the culture of that grain, and is often very abundant. It is found everywhere, appearing usually in abundance on the young plants in the fall; in the spring it is ordinarily the first rust to appear on cereal crops. No damage is usually attributed to it, and probably little or none is actually suffered, for the rye matures so early and the rust is so closely confined to the leaves that appreciable injury is almost always avoided. As with stem rust of rye, nothing can be predicted concerning the possibilities of leaf rust on spring rye, because comparatively little spring rye has been grown in this country up to the present time.

BOTANICAL CHARACTERISTICS, LIFE HISTORIES, AND PHYSIOLOGICAL SPECIALIZATIONS OF RUSTS.

GENERAL STATEMENT.

Investigations of recent years have shown conclusively that botanical characteristics, life histories, and physiological specialization of parasitic fungi vary to such an extent with the geographical distribution that a sequence of forms for one locality is not necessarily the sequence for any other. This brings us face to face with the problem of rust life histories in the United States. Although the European and American forms may be apparently identical morphologically, they are not necessarily identical in their life histories or physiological specialization. Investigations on the rusts in this country have shown that while the work of European botanists may be suggestive it can not be accepted as conclusive or final for the rusts of the United States without confirmatory experimental evidence. Some information has been gained in recent years on the specialization of the rusts growing on the different cereals, but much still remains to be done.

This bulletin represents an attempt to show briefly our present knowledge of these rusts in the United States in comparison with our knowledge of rusts in Europe. For detailed descriptions of the

European forms the reader is referred to the works of Eriksson and Henning, Klebahn, Ward, and others, cited later in this paper.

RELATIONSHIPS BETWEEN AMERICAN AND EUROPEAN FORMS.

Stem rust of wheat, rye, oats, and barley.—It has been known for more than 40 years that the stem rust (*Puccinia graminis* Pers.) of wheat, rye, oats, and barley in Europe may pass on to the barberry, producing æcidia, the cluster-cup stage, on this plant. The same has been likewise conclusively proved for the forms in this country. That the stem rust always does pass through the barberry stage in each season's sequence of forms, or that it can not live for more than one season without passing on to the barberry, is not only not implied but, as will be shown later, is absolutely disproved by field experience and experiment. We know that rust can live for more than one season without the intervention of the barberry, but we also know, on the other hand, that the barberry stage is not uncommon in many rust-infected districts, so that it may still be an important factor. This feature will be further discussed.

Leaf rust of wheat.—The æcidial stage of leaf rust (*Puccinia rubigo-vera tritici* Carleton) of wheat is not known either in Europe or in this country. Arthur (5) has shown that a similar rust on *Elymus virginicus* L. has a very common æcidium on the jewel weed (*Impatiens fulva* Nutt.). It can not be stated at present, therefore, whether this rust has an æcidium in this country, or whether it has entirely lost this stage, as seems to be the case with *Puccinia graminis* in Australia. It is a fact easily observed in almost any wheat area of the United States, at least as far north as St. Paul, Minn., and Fargo, N. Dak., that the uredo stage exists through the winter months in the severest winters and the rust may thus live independent of an æcidial stage.

Leaf (or crown) rust of oats.—In Europe the crown rust (*Puccinia coronata* Corda.) of oats has its æcidial stage on species of Rhamnus. The exact identity of the European and American forms may perhaps be open to doubt, though without question they are very closely related. It has been shown that in Europe two species of crown rust exist (62), one (*Puccinia coronata* Corda.) with æcidia on *Rhamnus frangula* L. and the other (*Puccinia coronifera* Kleb.)[1] with its æcidia on *Rhamnus cathartica* L. Neither of these æcidial host species are indigenous to this country, although they have been introduced and grown quite extensively as ornamental shrubs in different localities. The æcidia of our own rust on oats is found on *R. lanceolata* Pursh.,

[1] Eriksson on the basis of careful inoculation experiments has since separated the crown rusts into a large number of physiological species, dividing *Puccinia coronifera* Kleb. with its æcidium on *Rhamnus cathartica* into 8 physiological species and the *Puccinia coronata* (Corda.) Kleb. with its æcidium on *Rhamnus frangula* into 3 physiological species (49).

R. caroliniana Walt., and *R. cathartica* L. The exact relationship of the American and European crown rusts can be determined only by parallel inoculation experiments with European and American forms. These have not yet been performed.

Leaf rust of rye.—In Europe the leaf rust of rye (*Puccinia dispersa* Erikss.) forms its æcidium on *Anchusa officinalis* L. and *Lycopsis arvensis* L. Arthur (11, pp. 236, 237) succeeded once in growing the spermogonia of the American form (*Puccinia rubigo-vera secalis* Carleton) on *L. arvensis* L. in this country. It is believed, therefore, that the American and European forms are identical, but further experimental evidence should be obtained.

Leaf rust of barley.—Leaf rust (*Puccinia simplex* (Körn.) Erikss. and Henn.) of barley was not reported in the last bulletin on rust issued by this Bureau and seems, in fact, not to have been previously reported. The American form agrees in all morphological characteristics with the European form. It is chiefly characterized by the predominance of the one-celled teleutospores. The teleuto stage is often somewhat scarce. The earliest collection of this rust available for examination was obtained in Iowa in 1896. It was collected in California in 1905. It has been noticed in abundance, especially toward fall, chiefly on volunteer or very late barley, in Minnesota during the seasons of 1905 to 1908, in Maryland in 1910, and was reported in the spring of 1906 from Virginia, where it occurred in great abundance, but, like the leaf rust of wheat, it caused little appreciable damage.

BIOLOGIC FORMS.

General Discussion.

Rust fungi exhibit great variety in regard to complexity of life histories. Some are confined to single-host species, others range over two or more species of one host genus, while still others range over two or more genera and often on different tribes of the same family. This comprehensive range may obtain in addition to the alternation of host plants, as in the stem rust of cereals. For instance, the stem rust of oats passes its æcidial stage on barberry, while the uredo and teleuto stages may be found on practically all species and varieties of oats and on several grasses, some of which are not at all nearly related to oats, but are, in fact, genera of tribes somewhat removed from that of the oat (30, pp. 61–63). Attention must be called to the fact that the ranging to other species occurs most abundantly in the uredo and teleuto stages, though it is not unknown in the æcidial stage. Further complexity arises in the following way: What may appear to the the eye, and often under the highest power of the microscope, as one and the same species of rust on a number of species, or even varieties,

may really not be identical, since they are not interchangeable from one host to the other. For instance, the leaf rusts of wheat and rye can not be distinguished from each other under the best microscope lenses of the present day; yet the leaf rust of rye can not ordinarily be transferred by inoculation from rye to wheat and probably is not so transferred in nature. In other words, one finds here two fungi exactly similar in morphological characteristics, but physiologically different. These have been variously designated,[1] probably the most convenient and expressive term being "biologic forms." It is seen at a glance that the biologic forms may complicate very greatly the rust life history. They offer great difficulties to the investigator of rusts and, at the same time, are the basis for a most promising field of work of much importance, viz, the study of rust-resistant varieties.

A further complication arises from the facts obtained through experiments in various countries, which have shown that what is apparently the same species (the host being morphologically the same) may consist of a large number of strains or varieties which may behave differently in different geographic areas. The stem rusts of wheat and barley, for instance, are very similar, interchanging hosts easily and being capable of transfer to various grasses in this country. (See pp. 17–21; also Carleton, 30, pp. 54–56.) The researches of Eriksson (41, p. 70; 40, p. 294; 42, p. 500; 46, p. 198) show that in Sweden the stem rust of wheat goes with difficulty to barley and rye, while the stem rusts of barley and rye interchange hosts very easily. The chief factors in the complexity of the life history of cereal rusts may be summarized thus: (1) Alternation of hosts for different spore forms; that is, between the barberries and grasses. (2) The restrictions of different biologic forms of a single species of rust to various definite groups of host plants; as, for instance, *Puccinia graminis avenae* on oats; also found on Dactylis, etc., but not on wheat. (3) The variation of the biologic forms in different geographic areas.

The biologic forms of cereal rusts have been somewhat fully worked out by Eriksson and Henning, Klebahn, and others for various localities in Europe. The reader is referred to these authors for more complete details (39 and 63).

The forms in this country have received some attention, though scarcely as much as those in Europe. Practically the only work done in this line has been that of Hitchcock and Carleton (58) and of Carleton (30 and 31). The results of the latter agree in the main with the results recorded in this paper, but differ considerably

[1] Some of the terms used are Species sorores, Schröter (94, p. 69); biologische Spezies, Klebahn (62, pp. 232, 258); biologiske arter, Rostrup (88, p. 40); physiological species, Hitchcock and Carleton (58, p. 4); formae speciales, Eriksson (40, p. 292); Gewohnheitsrassen, Magnus (69, p. 82); and biologiske rassen, Rostrup (89, p. 116).

in some details. The tendency in recent years has been to consider the biologic forms of our rusts as somewhat closely limited to their host species. Hitchcock and Carleton (58) and Carleton (30) find the stem rust to contain the following forms:

(a) *Puccinia graminis tritici* Erikss. and Henn. on wheat, barley, *Koeleria cristata* (L.) Pers., *Festuca gigantea* (L.) Vill., *Agropyron richardsoni* Schrad., *Elymus canadensis glaucifolius* Muhl., *Elymus canadensis* L., *Hordeum jubatum* L., *Hordeum murinum* L., *Dactylis glomerata* L., *Agrostis alba* L., and *Agropyron tenerum* Vasey.

(b) *P. graminis avenae* Erikss. and Henn. on oats, several species. *Arrhenatherum elatius* (L.) Beauv., *Hordeum murinum* L., *Ammophila arenaria* (L.) Link., *Trisetum subspicatum* Beauv., *Dactylis glomerata* L., *Koeleria cristata* (L.) Pers., *Alopecurus alpestris*, *Holcus mollis*, *Agrostis scabra* Willd., *Polypogon monspeliensis* (L.) Desf., *Festuca* sp. indet., *Phleum asperum* Vill., *Bromus ciliatus* L., and *Eatonia obtusata* (Michx.) Gray.

Puccinia graminis secalis Erikss. and Henn. was not mentioned. Eriksson (41, p. 70; 40, p. 294; 42, p. 500; 46, p. 198; 44 and 47) finds them as follows:

(a) *P. graminis tritici* Erikss. and Henn. on wheat, sparingly on barley and rye.

(b) *P. graminis avenae* Erikss. and Henn. on oats, *Avena sterilis* L., *Avena brevis* Roth., *Arrhenatherum elatius* Mert. and Koch., *Dactylis glomerata* L., *Alopecurus pratensis* L., *Milium effusum* L., *Lamarckia aurea* Mch., *Bromus arvensis* L., *Trisetum distichophyllum* Beauv., *Bromus brachystachys* Horn., *Bromus madritensis* L., *Koeleria setacea* DC., *Festuca myurus* Ehrh., *Festuca tenuiflora* Sibth., *Festuca scinroides* Roth., *Phalaris canariensis* L., *Phleum asperum* Vill., and *Briza maxima* L.

(c) *P. graminis secalis* Erikss. and Henn. on rye, barley, *Hordeum jubatum* L., *Hordeum comosum* J. and Presl., *Bromus secalinus* L., *Elymus sibiricus* L., *Elymus arenarius* L., *Agropyron repens* Beauv., *Agropyron caninum* R. and Sch., and *Agropyron desertorum* Fisch.

The differences in results obtained by these European and American investigators have led the writers to examine further into the possibility of breaking down the barriers between the so-called biologic forms. This object, as will be seen below, has been accomplished without much difficulty, and at the same time considerable light has been shed on the true nature of the parasitism of cereal rusts.

Experiments on Biologic Forms.

Description of methods.

Rusts were collected in Minnesota and were transferred to their own host plants by artificial inoculations in the greenhouses at Washington, D. C. These constituted the stock rusts. In all the experiments the uredo stage was the spore form used. The cereal host plants were raised in small pots, about 10 plants to a pot, and inoculated in the seedling stage, either on the first or on the second leaf. The spores were placed on the leaf dry, or they were slightly moistened to enable them to adhere to the leaf surface. The plants were then sprayed with water by means of an atomizer until the leaf

surfaces were covered with very fine drops and then placed under large bell jars for two days. They were then removed from the bell jars to the greenhouse bench.

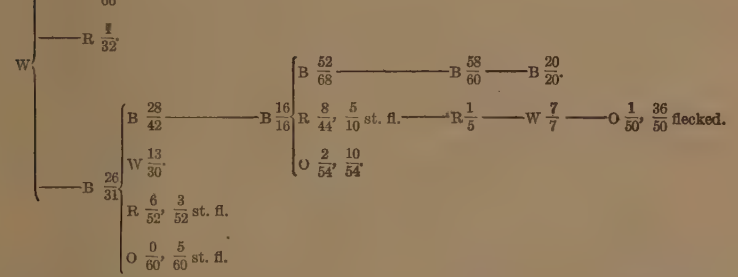
In the accompanying diagrams, W, B, O, and R represent wheat, barley, oats, and rye, respectively.[1] The succession of inoculations reads from left to right, the original host plant being on the extreme left. The figures in the form of a common fraction following each host plant are used as follows: (1) The numerator shows the number of leaves successfully infected; that is, leaves showing rust pustules. (2) The denominator shows the number of inoculated leaves. The fraction $\frac{7}{33}$, therefore, indicates 7 pustuled leaves out of a total of 33 inoculated. Again, the fraction $\frac{1}{3}$ followed by the word "flecked" indicates that 1 leaf out of 3 was flecked. The term flecked indicates a more or less close approach to the successful parasitism. The abbreviation "st. fl." means strongly flecked.

These diagrams show the results of various sets of inoculation experiments with the different grain rusts, on their own and other hosts, which have been carried on at different times.

EXPERIMENTS WITH BIOLOGIC FORMS OF STEM RUST.

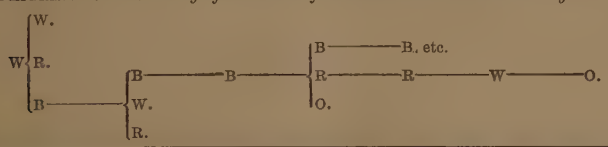
Diagrams 1, 2, 3, and 4 present summaries of inoculation experiments with *Puccinia graminis tritici* (stem rust) from wheat.

DIAGRAM 1.—*Summary of inoculation experiments with stem rust from wheat.*



The results indicated in diagram 1 are further summarized in diagram 2, which shows only the successful infections:

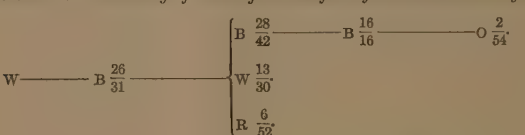
DIAGRAM 2.—*Summary of the successful inoculations shown in diagram 1.*



[1] Except in a few instances the grains used in these experiments were Preston wheat, Manchuria barley, Early Gothland oats, and spring rye, grown in Minnesota.

The wheat stem rust was carried directly to wheat, rye, and barley, but not to oats.[1] The figures show plainly that it goes with great ease to barley and wheat and very rarely (1 out of 32 inoculations) to rye. This rust can infect barley with about the same ease with which it goes to its own host. Although this may be interpreted as indicating the identity of barley and wheat stem rusts, it is not conclusive, since the barley rust behaves differently from the wheat rust toward the same cereals. When the wheat rust is taken to barley and then transferred to the other cereal hosts, it is seen that the barley has a decided influence on the rust. Diagram 3 summarized from diagram 1 shows its effect.

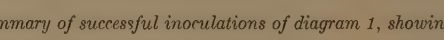
DIAGRAM 3.—*Summary of successful transfers of wheat rust through barley.*



The wheat rust from barley infects the wheat and barley again with great ease, and the rye with greater ease than the direct infection from wheat. Finally, from the second barley host the wheat rust may even infect oats, a result rarely obtained directly from wheat. In brief, the wheat rust, after passing on to barley, is capable of infecting all of the four cereals, but when transferred from the wheat without passing to barley, only barley and wheat are usually infected, rye being rarely infected and oats very rarely, indeed. Among the cereals, therefore, the stem rust of wheat in this country is not confined to wheat as closely as Eriksson has found it to be in Sweden, nor is it confined to barley and wheat, as found by Carleton.

Diagram 4, summarized from diagram 1, shows the actual course of infection of wheat rust taken, in succession, on all of the small grains.

DIAGRAM 4.—*Summary of successful inoculations of diagram 1, showing succession.*



The effect on the wheat-rust parasite when barley is taken as a host is clearly shown to be that of enabling a wider range of infection. An interesting feature of this diagram is seen in the fact that the final successful inoculation of oats was directly from the wheat, but the rust had previously passed on to three barley plants and two rye plants.

Diagrams 5 to 10, inclusive, present summaries of inoculation experiments with *Puccinia graminis hordei* (stem rust) from barley.

[1] Mr. H. B. Derr, of the United States Department of Agriculture, reports having obtained in the laboratory the following successful inoculations: W —>O —>B —>O —>O. The number of successful infections in each case was not recorded.

DIAGRAM 5.—*Summary of inoculation experiments with stem rust from barley.*

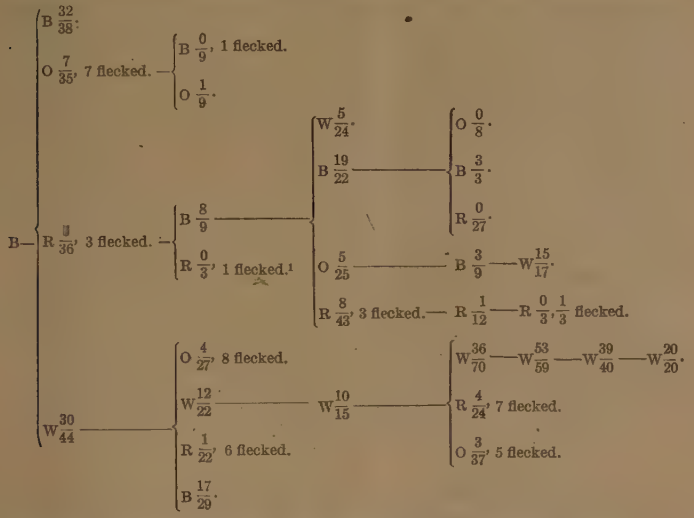
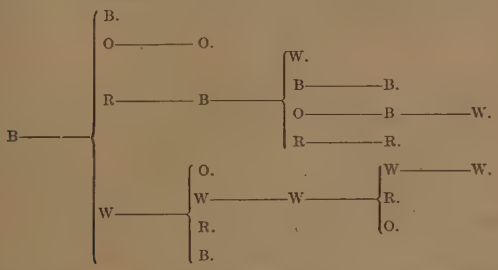


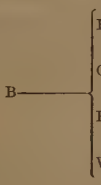
Diagram 6 summarizes the successful infections shown in diagram 5.

DIAGRAM 6.—*Summary of successful inoculations shown in diagram 5.*



The barley rust is seen at a glance to be more versatile than wheat rust. All four cereals are directly infected by this rust, as shown by diagram 7.

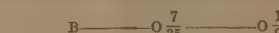
DIAGRAM 7.—*Summary of successful direct inoculations of stem rust of barley.*



[1] Eaten by slug.

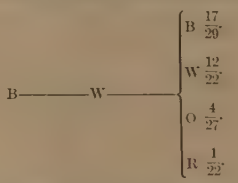
The stem rust of barley, like that of wheat, goes with equal ease on barley and wheat. Rye is more easily infected by barley rust than by the wheat rust. Oats are capable of direct infection by barley rust. The oat pustules were very small and weak, and thus precluded the possibility of very numerous experiments with the barley rust from oats; but diagram 5 shows that successful infections were obtained as follows:

DIAGRAM 8.—*Summary of successful inoculations of oats with stem rust of barley.*



The barley rust, after being transferred to rye, was carried to barley and then to all of the four cereals; it was likewise transferred to wheat and then to the other cereals. The rye and wheat rusts, as shown by other diagrams, are usually incapable of direct transfer in this manner. That the barley rust is carried through wheat and then transferred to the other cereals is shown in diagram 9 summarized from diagram 5:

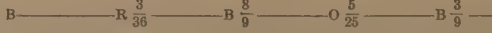
DIAGRAM 9.—*Summary of transfer of stem rust of barley through wheat to other cereals.*



The barley rust, then, after passing through rye and wheat, is still able to infect all four cereals.

Diagram 10, summarized from diagram 5, shows that barley rust was successfully transferred to all of the four cereals.

DIAGRAM 10.—*Summary of transfers of stem rust of barley directly to other cereals.*



The comparatively large percentages of infection obtained are probably accounted for by the fact that in each case barley intervened as a host between rye and oats and between oats and wheat.

The barley stem rust enjoys the widest range of any of the biologic forms of the cereal rusts. On the other hand, a transfer of any of the other stem rusts to barley widens the range of that rust. We have here, then, a decided reaction of host upon parasite, enabling the latter to adapt itself to hosts not ordinarily congenial; for instance, W——>B——>O.

As shown under wheat rust, the barley rust and wheat rust are seen to be not necessarily identical, though the fact that they are

but slightly changed forms of the same species can not be doubted. Although they infect barley and wheat plants with almost equal ease, they behave differently in the other inoculations. That this difference may be attributed to the influence of host on the parasite is clear from the fact that wheat rust after passing to barley behaves in a similar manner to the barley rust, although the latter retains a more versatile character even after passing to the other host plants. Table II (p. 26) throws further light on the relationships of wheat and barley rusts. Diagrams 11 and 12 summarize the inoculation experiments with *Puccinia graminis secalis* (stem rust) from rye.

DIAGRAM 11.—*Summary of inoculation experiments with stem rust from rye.*

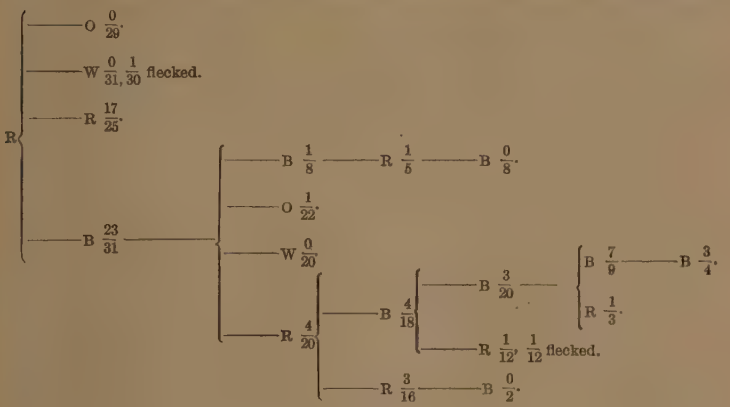
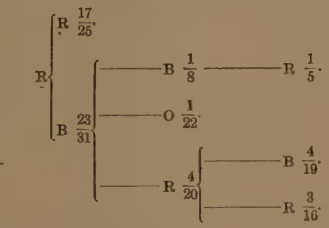


DIAGRAM 12.—*Summary of the important results shown in diagram 11.*



The rye rust infects rye and barley with about equal ease; in fact, the proportion of successful inoculations indicates even greater preference for barley than for rye, though a much larger number of inoculations would be necessary to decide this point conclusively. Wheat is rarely directly infected. Derr reports having obtained the successful infection of rye rust to wheat in a few instances. These infections were not obtained directly, but 1 out of 22 inoculations was successful after the rye rust had passed to barley. In our own

experiments no infections to wheat after barley and only one to oats after barley were obtained with the rye rust, but only a small number of attempts on wheat and oats were made from the rust on barley. There is little doubt that rye rust can be made to go to wheat after passing to barley, as has been shown by Derr's experiments previously cited. Diagram 13, summarized from diagram 11, shows the direct infections obtained with stem rust from rye.

DIAGRAM 13.—*Summary of the direct inoculations of barley and rye with stem rust from rye.*

Diagram 14 shows the possibility of infection of all four cereals by passing to barley.

DIAGRAM 14.—*Summary of inoculations by stem rust of rye directly to two cereals and through barley to wheat and oats.*

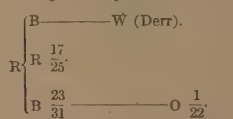


Diagram 15 presents a summary of inoculation experiments with *Puccinia graminis avenae* (stem rust) from oats:

DIAGRAM 15.—*Summary of inoculation experiments with stem rust from oats.*

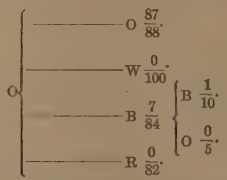
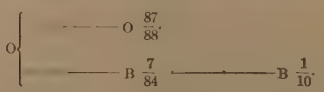
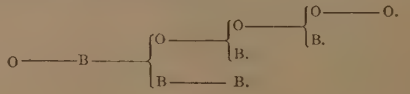


Diagram 16 presents a summary of the successful infections[1] shown in diagram 15.

DIAGRAM 16.—*Summary of successful inoculations shown in diagram 15.*



[1] Derr reports having obtained a direct infection of oats to wheat and one of oats to rye. In the case of the wheat the rust was further transferred as follows: O—>W—>B—>W. He also further carried the oats to barley and transferred infection as follows:



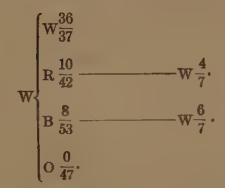
The number of successful inoculations of stem rust of oats to wheat and rye has been insufficient to make absolute statements concerning them, but there is little doubt that under highly favorable conditions they can be made. On the other hand, there is no doubt that the oat rust can be carried to barley and from barley to either oats or barley, as a large number of successful trials by Derr have shown. In all cases the pustules obtained in the course of the inoculations were small and weak and the rust was very evidently not on a congenial host. The oat rust is thus seen to be the most closely specialized of the biologic forms of *Puccinia graminis* on the small grains, but in its ability to infect the other species under rarely occurring conditions still shows its close affinity to the other rusts. Of all the stem rusts on the small grains that of oats is the most distinctive and individualistic in appearance, having larger pustules of uredo spores which are formed very commonly both on stems and leaves (as in barley), in sharp contrast with the more restricted location of the pustules in the rusts of wheat and rye. As a biologic form, the stem rust of oats may be said to be generally confined to oats. It can at times be carried to barley, but never produces large or vigorous pustules. It is only rarely that the transfers to wheat and rye can be made.

EXPERIMENTS WITH BIOLOGIC FORMS OF LEAF RUST.

Fewer experiments have been made with the biologic forms of leaf rusts than with the stem rusts, but these experiments indicate that, as a rule, the leaf rusts are not as versatile as the stem rusts, being confined more closely to the original hosts.

Diagram 17 presents a summary of inoculation experiments with *Puccinia rubigo-vera tritici* (leaf rust) from wheat.

DIAGRAM 17.—*Summary of inoculation experiments with leaf rust from wheat.*



The leaf rust of wheat was carried directly to wheat, rye, and barley, but in 47 inoculations it would not transfer to oats. It is similar to *Puccinia graminis tritici*, which can easily be transferred to the first two cereals, to rye rarely, and to oats only in very exceptional instances. But the leaf rust of wheat will not infect barley nearly as readily as the stem rust of wheat, but seems to transfer to rye more easily than the stem rust. No experiments were made

to determine whether or not this rust goes more easily to the other cereals after having been grown on barley, as is the case with the stem rust of wheat. Carleton (30, p. 20) reports negative results with *Puccinia rubigo-vera tritici* in inoculations on oats, barley, and rye. This indicates either that the strain of rust which he used for his inoculations may have been slightly different from the strains used in our inoculations, or that the conditions were not as favorable for infection. Such a difference in strains, perhaps, may exist in the same species of rust gathered from different localities even in the same country.

Diagram 18 presents a summary of inoculation experiments with *Puccinia simplex* (leaf rust) from barley.

DIAGRAM 18.—*Summary of inoculation experiments with leaf rust from barley.*

B { W $\frac{0}{49}$. R $\frac{0}{37}$. B $\frac{44}{46}$. O $\frac{0}{50}$.

These experiments indicate that the leaf rust of barley is closely confined to the one host, barley, as no infection took place on either wheat, rye, or oats in a large number of inoculations on each. In this particular it is very different from the stem rust of barley, which may be transferred to the other three cereals.

Diagram 19 presents a summary of inoculation experiments with *Puccinia rubigo-vera secalis* (leaf rust) from rye.

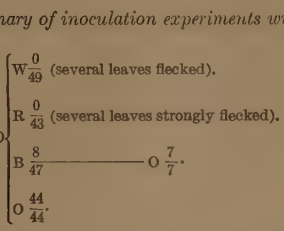
DIAGRAM 19.—*Summary of inoculation experiments with leaf rust from rye.*

R { W $\frac{0}{48}$ (most leaves flecked). R $\frac{33}{35}$. B $\frac{0}{50}$ (many leaves flecked O $\frac{0}{46}$.

The leaf rust of rye is also highly specialized and in numerous inoculations did not transfer to the other cereals. Carleton's results (30, p. 43) in numerous trials are identical. The flecking of the wheat and barley showed that they were infected with the rust, but that extensive development of the rust mycelium did not take place. The rye stem rust, on the other hand, easily transfers from rye to barley.

Diagram 20 presents a summary of inoculation experiments with *Puccinia coronata* (leaf rust) from oats.

DIAGRAM 20.—*Summary of inoculation experiments with leaf rust from oats.*



Although highly specialized, the leaf rust of oats can be transferred to barley, but it did not transfer to either wheat or rye. The effect of barley on it was not determined, except to show that from barley to oats the rust in a few trials transferred as easily as from oats to oats. In Carleton's experiments (30, p. 46) inoculation with this rust on barley gave negative results.

In many of the experiments on biologic forms previously cited, it was noticeable that the same rust species would not give the same percentage of infection on various hosts if the inoculations were made from rusts gathered in different localities. This may account for the diverse results of different investigators and leads to the belief that there may be a large number of strains of a rust species, none of which will act exactly like another toward the same hosts. Undoubtedly by variation and adaptation to varying conditions a certain rust species, widely distributed, may form a large number of strains or types which, when this process has been continued for a considerable time, differ widely in their physiological reactions. These may become the physiological or "biologic" species.

EFFECT OF CHANGE OF HOST ON THE MORPHOLOGY OF THE UREDOSPORE.

In experimental cultivation of *Puccinia graminis tritici* from wheat on barley and *Puccinia graminis hordei* from barley on wheat it was found that there existed a slight morphological difference between the uredospores of the stem rust of barley and the stem rust of wheat. Upon closer examination this difference seemed to be measurable—that is, the uredospores of barley measured (on a basis of measurement of 50 spores, widely selected) considerably shorter and very slightly narrower than those on wheat. An experiment was therefore inaugurated to determine what the effect would be on the size of the spores of the barley rust when grown on wheat and of the wheat rust when grown on barley. Transfers were accordingly made of the barley rust to two pots of wheat and of the wheat rust to two pots of barley. The barley rust on wheat was then transferred to wheat plants continuously for about a year, and the wheat rust in a similar manner was grown on barley. The rust in each pair of pots was transferred to two other pots, so that two separate strains were

kept continuously for check purposes. All precautions possible to ordinary greenhouse work were taken to avoid accidental infection and the mixing of cultures. The results given in the table below show the measurements of (1) the original material—that is, of barley rust on barley and wheat rust on wheat; (2) the same rusts after 6 inoculations had been made on new hosts; and (3) after 17 inoculations, covering a period of almost one year. The spore measurements were carefully made from typical spores. Where 50 spores were measured, they were taken from at least 5 different pustules and from 2 or 3 leaves. Where 10 were used they were selected from normal, mature pustules. The difference in size between spores from mature and immature pustules is quite marked, the immature being smaller than the mature. As the variation in width of the spores from different hosts is very slight, measurements of 10 may show a small difference from the measurement of 10 original spores toward either plus or minus.

TABLE II.—*Change in morphology of the uredospores by cultivation of stem rust from wheat on barley and from barley on wheat.*

Description of culture.	Date of collection of spores.	Number of spores measured.	Spore measurements, original material (μ).		Number of intervening inoculations.	Date of collection.	Number of spores measured.	Spore measurements (μ).			
								Cultivated material.		Difference (compared with original material).	
			Width.	Length.				Width.	Length.	Width.	Length.
	1906.					1907.					
Wheat rust transferred to and grown continuously on barley	Nov. 13 and Nov. 14	50	18.15	31.33	6	Feb. 28	10	18.17	30.13	+0.02	−1.20
					17	Sept. 26	50	17.52	29.01	− .63	−2.32
Barley rust transferred to and grown continuously on wheat	Nov. 14 and Nov. 22	50	17.46	28.51	6	Feb. 28	10	17.53	30.22	+ .07	+1.71
					17	Sept. 26	50	17.67	31.12	+ .21	+2.61

This table shows that in the original material the wheat-rust uredospores are 0.69 μ wider and 2.82 μ longer than the corresponding barley-rust spores. As stated above, the difference in width is too small (a little more than 0.5 μ) to allow of safe conclusions as to its variations. After 6 successive infections of each rust on the other host, the wheat rust had lost an average of 1.2 μ in length, the width remaining practically the same (+0.02 μ). The barley rust, on the other hand, had gained in length 1.71 μ, the width running practically the same (+0.07 μ). The two rusts at this time gave almost identical measurements, viz, wheat rust on barley 18.17 μ by 30.13 μ and barley rust on wheat 17.53 μ by 30.22 μ. After 17 successive intervening inoculations (almost a year from the time of the collection

of the original material) the wheat rust on barley had lost from the original material 0.63 μ in width (practically negligible) and 2.32 μ in length, while the barley rust on wheat had gained 0.21 μ in width (again practically negligible) and 2.61 μ in length. If these measurements are compared with those of the original material it will be seen that the wheat rust on barley has decreased in spore size to almost exactly that of the original barley rust and the barley rust on wheat has increased in spore size to nearly that of the original rust on wheat, as follows:

Original wheat rust	18.15 μ by 31.33 μ.
Barley rust after 10 months on wheat	17.67 μ by 31.12 μ.
Original barley rust	17.46 μ by 28.51 μ.
Wheat rust after 10 months on barley	17.52 μ by 29.01 μ.

Although these differences are not great, they seem sufficient to indicate that the host plant exercises not only a decided physiological and biological reaction upon the parasite but that it may, even in such a short period as one year, exert a measureable effect on the morphology.[1] It has already been shown (p. 17) that wheat rust if first transferred to barley may be transferred to oats with considerable ease, thus showing the physiologic change going hand in hand with the morphologic change.

GENERAL SUMMARY OF CONCLUSIONS DERIVED FROM EXPERIMENTS ON BIOLOGIC FORMS.

In summarizing, the following points in regard to biologic forms of rusts of cereals may be emphasized:

(1) *Puccinia graminis tritici* Erikss. and Henn. (stem rust of wheat), *P. graminis hordei* F. and J. (stem rust of barley), *P. graminis secalis* Erikss. and Henn. (stem rust of rye), and *P. graminis avenae* Erikss. and Henn. (stem rust of oats) are undoubtedly biologic forms of the same species *Puccinia graminis* Pers.

(2) These forms are not entirely confined to their respective hosts, but vary in range in part according to the host plants they have been recently inhabiting.

(3) *P. rubigo-vera tritici* Carleton (leaf rust of wheat) and *P. rubigo-vera secalis* Carleton (leaf rust of rye) are more highly specialized than the corresponding stem rusts.

(4) *P. graminis hordei* (stem rust of barley) has ordinarily the widest range, while *Puccinia simplex* Erikss. and Henn. (leaf rust of barley) and *P. rubigo-vera secalis* (leaf rust of rye) have more restricted ranges.

(5) Under very favorable conditions, particularly after first transferring to barley, all the stem rusts can be carried successfully to the other cereals.

(6) When the rusts are transferred to uncongenial hosts and produce pustules on these, the pustules are almost invariably minute and weak, producing comparatively few spores. Some pustules apparently never open. The congenial hosts of each rust may be summarized as follows:

P. graminis tritici (stem rust of wheat) on wheat and barley.

[1] Evans (50, p. 461) has shown previously that many of the biologic forms of the genus Puccinia can be distinguished by slight differences in morphology of the early uredo mycelium, particularly in the formation of the substomatal vesicle.

P. graminis hordei (stem rust of barley) on barley, wheat, and rye.
P. graminis secalis (stem rust of rye) on rye and barley.
P. graminis avenae (stem rust of oats) on oats.
P. rubigo-vera tritici (leaf rust of wheat) on wheat.
P. simplex (leaf rust of barley) on barley.
P. rubigo-vera secalis (leaf rust of rye) on rye.
P. coronata (leaf rust of oats) on oats.

(7) Two biologic forms may inhabit the same cereal or cereals (for instance, wheat and barley rusts on wheat and barley) without being identical.

(8) By gradual variation and adaptation to varying conditions a certain rust species, widely distributed, may form a number of strains or types, differing in physiological reactions.

(9) The host plants exercise a strong influence, not only on the physiological and biological relationships, but in some cases even on the morphology of the uredospores.

In regard to the relationships of the cereal rust forms to the numerous grass rusts of the United States there is much to be done. A beginning has been made, and experiments have been performed confirming Carleton's results (30, pp. 55, 61–63) in regard to the infection of *Hordeum jubatum* with the stem rusts of wheat and barley and orchard grass with the stem rust of oats. That *Agropyron repens* also acts as host for the stem rust of wheat has been proved. The relationship of *Puccinia phlei-pratensis* to other rusts has been investigated and a summary of results published (59, p. 791). The importance of this phase of the biologic forms of cereal rusts is very great and demands early attention. The most extensive results obtained up to the present time are those of Carleton with the American and Eriksson with the European rusts.[1]

THE ÆCIDIAL STAGE OF RUSTS.

HISTORY OF BARBERRIES IN RELATION TO RUST.

Up to 1864–65, when De Bary demonstrated the heteræcism of *Puccinia graminis* Pers., rust life histories were very incompletely

[1] During the course of preparation of this bulletin several important papers have appeared throwing further light on biologic forms of rust. J. C. Arthur ("Cultures of Uredineæ in 1909," Mycologia, vol. 2, no. 5, 1910, pp. 227, 228) cites experiments of his own showing that *Puccinia poculiformis* (Jacq.) Wettst. (*P. graminis* Pers.) has been grown on *Triticum vulgare* from æcidiospores derived from inoculations on *Berberis vulgaris* with teleutospores from *Agropyron repens, A. tenerum, A. pseudorepens, Agrostis alba, Cinna arundinacea, Elymus canandensis,* and *Sitanion longifolium,* respectively. He concludes that "although in the uredinial stage this rust shows racial strains that inhibit the ready transfer from one species of host to another * * * yet in the æcial stage racial strains play no part, and the barberry acts as a bridging host between each and every other gramineous host."

Jaczewski, on the other hand, in a recent article (Zeitschrift für Pflanzenkrankheiten, vol. 20, no. 6, 1910, pp. 356, 357) cites comprehensive inoculation experiments to show that the stem rusts of grains and grasses in Russia as a rule are not interchangeable even with the barberry as a bridging host, but retain distinct physiological specialization in the æcidial as well as in the uredo stage. He also shows that the æcidia produced from inoculations with the teleutospores from the stem rusts of wheat and barley, respectively, behave differently when used for inoculation on the same series of grains and grasses, and he believes it easily possible that the stem rust on barley is a distinct physiological species, a conclusion independently derived in another way by the writers of this bulletin (pp. 17–20 and 25–27). Although it is evident from the experiments cited by Arthur that the barberry may act as a bridging host for rusts between some gramineous hosts, in the light of the work of Jaczewski and others it seems that further experimentation on a large number of rusts is necessary before the sweeping statement that "in the æcial stage racial strains play no part" can be generally accepted.

understood. That the proximity of barberries to grainfields was injurious to the crops had long been believed, although no one could say just what caused the damage. In many cases stringent laws making the destruction of barberries compulsory had been enacted. Klebahn (63, p. 205) finds the first mention of such legislation by De Magneville (68, p. 18), who says that laws against the growing of barberries were extant in Rouen, France, in 1660. The citations of Loverdo (67, p. 199) and Prillieux (86, p. 221) undoubtedly are taken from this reference. Klebahn, however, was unable to locate the original law, even though M. Ch. de Beaurepaire, Archiviste Paleographe de la Prefecture de la Seine Inferieure in Rouen, looked through the record of laws for 1660 and also for 1760. There is, thus, some doubt about this report.

In the eighteenth century rust literature became much more extensive. According to Klebahn (63, pp. 205, 206), Erhart (38, p. 59) says that in 1720 an English farmer destroyed his neighbor's barberries with hot water because they hurt his wheat. This instance is also cited by Hornemann (56, p. 8). De Bary (12, p. 35) found the noxiousness (Schädlichkeit) of barberry to wheat mentioned by Krünitz (65, p. 198), who says:

> Man hat sie ohne Grund beschuldigt, dass sie in den nahe dabei stehenden Korn den Brand verursachten, weswegen dieselben sogar aus den Zaünen um die Landgüter verbannt werden.

Withering (105, p. 199) in 1776 wrote:

> This shrub should never be permitted to grow in corn lands, for the ears of wheat that grow near it never fill, and its influence in this respect has been known to extend as far as 300 or 400 yards across a field.

According to Davis (37, p. 82) the oldest legislation in the United States concerning barberries was enacted in Connecticut in 1726, when towns were empowered to pass regulations at their town meetings for the destruction of barberries within their respective townships, "it being by plentiful experience found that where they are in large quantities they do occasion, or at least increase, the blast on all sorts of English grain." In Massachusetts an act was passed in 1755 making the destruction of barberries in that Colony before June 13, 1760, compulsory (73, pp. 797, 798) because "it has been found by experience that the blasting of wheat and other English grain is often occasioned by barberry bushes to the great loss and damage of the inhabitants of this province." Similar laws, but much less stringent than those of Massachusetts, were passed in Rhode Island in 1766 and 1772, and again in Connecticut in 1779.

In 1781–1784 Marshall (71, pp. 19, 359; 72, p. 11), by reason of the strong existing prejudice against barberries in England, undertook actual experiments to determine whether or not barberries were the

cause of rust in grain. In February, 1782, he planted a barberry bush in the middle of a wheat field. He states that a little before harvest:

> The wheat was changing and the rest of the piece (about 20 acres) had acquired a considerable degree of whiteness (white wheat), while about the barberry bush there appeared a long but somewhat oval-shaped stripe of a dark, livid color, obvious to a person riding on the roadside at a considerable distance.

Marshall continues as follows:

> The part affected resembled the tail of a comet, the bush itself representing the nucleus, on one side of which the sensible effect reached about 20 yards, the tail pointing toward the southwest, so that probably the effect took place during a northeast wind.
>
> At harvest, the ears near the bush stood erect, handling soft and chaffy; the grains slender, shriveled, and light. As the distance from the bush increased the effect was less discernible, until it vanished imperceptibly.
>
> The rest of the piece was a tolerable crop and the straw clean, except on a part which was lodged, where the straw nearly resembled that about the barberry; but the grain on that part, though lodged, was much heavier than it was on this, where the crop stood erect.
>
> The grain of the crop, in general, was thin bodied; nevertheless, 10 grains, chosen impartially out of the ordinary corn of the piece, took 24 of the barberried grains, chosen equally impartially, to balance them.

This experiment was repeated by Marshall in Staffordshire with similar results, and he became more firmly than ever of the opinion that barberry was injurious to wheat.

In 1787 Withering (106, p. 366) in speaking of *Berberis vulgaris* repeated the statement which he made in 1776, already quoted (p. 29).

According to Windt (104), Schöpf (93, p. 56) in 1788 said that in America the barberries in proximity to fields were blamed for injuring grains and other field crops. Just how the injury was caused no one could say.

A severe epidemic of "mildew" took place in England in 1804 (84, p. 51). Arthur Young, secretary of the board of agriculture at that time, issued a circular asking for information as to the cause of "mildew" in wheat. In answer to the question "Have you made any observations on the barberry as locally affecting wheat?" numerous correspondents reported that injury resulted wherever barberries occurred near a wheat field. According to the same authority, Sir Joseph Banks (14, p. 521) in 1805 said: "Is it not more than possible that the parasitic fungus of the barberry and that of wheat are one and the same species, and that the seed is transferred from the barberry to the corn?"

In 1806 Windt (104, p. 8), from his own observations and experiments, came to the conclusion that the barberry was the cause of rust in wheat and that it acted as a center of infection.

Thomas A. Knight, president of the Royal Horticultural Society of London, in 1813 recognized the importance both of the uredo stage and of the barberry. He says (64, p. 85):

> A single acre of mildewed wheat would probably afford seeds sufficient to communicate disease to every acre of wheat in the British Empire, under circumstances favorable to the growth of the fungus.

Knight adds:

> There is also reason to believe that the barberry tree communicates this disease to wheat, and I have also often noticed a similar apparent parasitical fungus upon the straws of the couch-grass in the hedges of cornfields.

In 1818 a paper was published by the Royal Agricultural Society of Denmark, which was the result of investigations by Schoeler (92, p. 289) in Denmark from 1807 to 1816. He had planted grains around barberries and found that rye and oats were liable to be destroyed every year by rust; that when large and small barberry bushes were planted in his field—

> The larger bushes did not give rise to rust when they lost their foliage in the process of transplanting, but, on the contrary, the smaller bushes, which did not lose their leaves so readily, did give rise to the rust in rye to a very marked degree.

In 1816 Schoeler actually cut freshly rusted barberry leaves, carried them in a box into a rye field, and rubbed them on rye plants moist with dew. The plants were carefully marked and in five days were found to be severely affected with rust, "while at the same time not one rusty plant could be found anywhere else in the field."

A German farmer performed similar experiments in 1818 (77, p. 280; 52, p. 408). He gathered the dust (Staube) which fell from the cup (Kapsel) on barberry leaves as he shook them and placed it on rye plants far from the rye fields and where there were no barberries in the neighborhood. After five or six days the plants thus treated were attacked by rust, while there was nothing similar on any other plants. He concluded that the dust from barberries blown by the wind to grains causes the rust.

While many botanists still believed that the rusts on barberry and wheat belonged to different genera, some were sufficiently good observers to believe that the Puccinia and Uredo were in some way connected. In 1852 Tulasne (97, pp. 79–113) proved the genetic relation between the summer rust (Uredo) and the autumn rust (Puccinia) and also showed (97, p. 141) that the autumn spores of many of the rust species, among which are *Puccinia graminis* and *P. coronata*, go through a resting period from autumn until spring before they will germinate.

It remained for De Bary, in 1864–65, to publish the results of his experiments, which actually proved heterœcism of *Puccinia graminis* (12, pp. 15–49). He demonstrated in 1864 that the sporidia from

teleutospores from *Agropyron repens* Beauv. and *Poa pratensis* L. would give rise to the æcidia on Berberis and, in 1865, that æcidiospores from Berberis sown on rye would produce uredospores and later teleutospores. He did not stop here, but kept at work on other rusts, and in 1865 showed that *Puccinia coronata* has its æcidium on *Rhamnus frangula* and *P. rubigo-vera* its æcidium on *Lycopsis arvensis*. From this time on, life-history work on the Uredineæ has made rapid strides and the connection of one æcidial form after the other has been discovered by such men as Oersted, Fuckel, Magnus, Schröter, Wolff, Rostrup, Winter, Nielsen, Reichardt, Hartig, Rathway, Cornu, Plowright, Farlow, Barclay, Thaxter, Eriksson, Klebahn, Arthur, Holway, Kellerman, and others.[1]

In 1884 Plowright produced successful infection on Berberis with rust from teleutospore material from *Agropyron repens* sent by Arthur from the United States, and Bolley produced successful infection on barberry with teleutospore material from wheat in 1889 (1, p. 395). Carleton (30, p. 54) produced successful infection on barley from æcidiospores from Berberis. These experiments have been repeated by Arthur time and again and have been performed by the authors. They prove that the *Puccinia graminis* in America is the same species as the *P. graminis* in Europe, although the physiological specializations and consequent biologic forms are different in the two countries.

More work has been done on *Puccinia graminis* than on any other rust fungus, and its relationship to the æcidium on several species of Berberis has been proved repeatedly by Eriksson. Species of Mahonia have also been proved to be æcidial hosts of this rust (85, p. 234; 13, p. 96).

The relationships of *Puccinia graminis* on oats and rye to the æcidium on species of Berberis and the relations of *P. coronata* to the æcidium on species of Rhamnus have also been demonstrated, while the æcidial forms of the other leaf rusts are not known. This has led again to the mooted question whether or not the æcidial stage is necessary in the life history of rusts, and, if not absolutely necessary, what function the æcidial stage fills.

FUNCTIONS OF THE ÆCIDIUM.

General Discussion.

As early as 1882 Plowright (85, p. 234) questioned whether the æcidium is an essential stage in the life history of rusts and grasses, and gave as his principal reason for raising this question the apparent

[1] For citations of literature see Plowright (84), 1889; Eriksson and Henning (39), 1894; Klebahn (63), 1904; McAlpine (76), 1906; Arthur (2, 4–11), 1899–1909.

"disproportion which exists in England between the amount of of mildew (rust) and the number of barberries." He further states that there is a wonderful difference between the extent of injury caused by "mildew" when derived directly from the barberry and when derived from a uredo that has reproduced itself through several generations, the former being much greater than the latter. He adds:

> This is only what one would expect when the fact is taken into consideration that the æcidium spore is a sexual product, whereas the uredospore is not.

Bolley (21, p. 12) holds a similar view and says:

> The services rendered by it [the barberry] should probably be considered as that of reinvigoration, much the same as that which is rendered by reproduction in ordinary plants.

Arthur (3, pp. 67–69) similarly believes the æcidium is a device to restore vigor to the rust fungus, the æcidiospore giving rise "to a much more vigorous state of the fungus than the uredospores do," and, as a consequence, the prevention of the production of the æcidiospore by the removal of the æcidial host would reduce very largely the injury which the rust is capable of producing.

This view has been greatly strengthened since Blackman's (18) discoveries of cell fusions and the origin of the binucleated condition in the æcidium of *Phragmidium violaceum* on *Rubus fruticosus* and *Gymnosporangium clavariaeforme* on Crataegus and in the further studies of Christman (33 and 34), Blackman and Fraser (19), and Olive (79 and 80), all of whom have shown that in various rust species a cell fusion takes place and the consequent binucleated condition arises at the base of the æcidium. The authors differ in certain instances as to the details of this fusion, and in the species studied, but generally agree that this fusion is sexual. If it is functionally a sexual union the final step of which is the nuclear fusion in the teleutospore,[1] the reinvigoration of the rust as claimed by Plowright, Bolley, and Arthur is to be expected as a natural consequence.

Experiments to Determine the Vitality of Successive Uredo Generations of Various Grain Rusts.

Material used and methods employed.

To test this invigoration theory in part and to determine, if possible, whether or not the æcidial stage is necessary in the life history of rusts, continuous cultural experiments from the uredospore of the various cereal rusts were undertaken by the authors in 1907 and

[1] Dangeard and Sapin-Trouffy demonstrated the nuclear fusion in the teleutospore of rusts as early as 1893 (Comptes Rendus 116, pp. 267-269 and 1304–1306) and regarded this a "pseudofecundation." These studies led to further investigations on the sexuality of the Uredineæ and consequent discovery of cell fusion in the æcidium.

were carried without a break until August, 1909. In these experiments 52 generations of uredospores were grown without the intervention of any other spore form. These generations consisted of *Puccinia graminis* on wheat, barley, and oats; *P. rubigo-vera* on wheat and rye; *P. simplex* on barley; *P. graminis*, originally from barley, on wheat; and *P. graminis*, originally from wheat, on barley. At the end of these experiments cultures were as easily made and the rusts grew as luxuriantly as at the first inoculation with material obtained directly from the field.

In these experiments care was taken to avoid accidental infection from outside sources. Plants showing indications of such infection were destroyed. As far as possible series of 10 plants were used and each inoculation was made with material from separate leaves of the stock plants. The source plants were always maintained until evidence of successful infection appeared. If infection did not take place by reason of unfavorable conditions at the time of inoculation, inoculations were again made from the source plants. For instance, if A was used to inoculate B, A was not destroyed until B showed fresh pustules. If B gave no evidence of the presence of rust, another B was inoculated from A. The following rusts were used: *Puccinia graminis* on wheat, *P. graminis* on oats, *P. graminis* on barley, *P. graminis* on rye, *P. rubigo-vera* on wheat, *P. simplex* on barley, *P. coronata* on oats, and *P. rubigo-vera* on rye.

The original source material was brought from the Minnesota Agricultural Experiment Station, October 5, 1906. Between that date and February 6, 1907, at least four transfers were made, probably as many as six or eight. During a part of the time the series were run at Minnesota and the remainder of the time at Washington, D. C. When transfers were to be made, heavily pustuled leaves were picked, inclosed in envelopes, and sent by mail. Inoculations were made on their arrival at their destination. Infection almost invariably took place readily. The transfers were necessary by reason of change of location of the men in charge of the experiments.

SUMMARIES OF THE EXPERIMENTS.

The following tables give the dates when all inoculations were made as well as the number of successful infections from each inoculation:

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts.*

PUCCINIA GRAMINIS TRITICI ON WHEAT.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[1] 10	a	Feb. 6	10	Feb. 19	[1] 7
B	Feb. 19	10	Mar. 5	[1] 10	b	Feb. 19	10	Mar. 5	[1] 8
C	Mar. 5	10	Mar. 21	[1] 10	c	Mar. 5	10	Mar. 21	[1] 10
D[2]	Mar. 26	10	Apr. 8	10	d[2]	Mar. 26	10	Apr. 8	10
E	Apr. 17	[3] 10	May 7	5	e	Apr. 19	[4] 10	May 7	9
F	May 8	10	May 27	[5] +5	f	May 8	10	May 27	[5] +5
G	May 28	10	June 13	[5] +5	g	May 28	10	June 13	[5] +5
H	June 14	10	June 25	[5] +7	h	June 14	10	June 25	[5] +7
I	June 25	10	July 8	10	i	June 25	8	July 8	8
J	July 8	10	July 23	6	j	July 8	10	July 23	4
K	July 24	10	Aug. 6	10	k	July 24	10	Aug. 6	10
L	Aug. 7	10	Aug. 21	10	l	Aug. 7	10	Aug. 21	10
M	Aug. 22	10	Sept. 8	10	m	Aug. 22	10	Sept. 8	10
N	Sept. 9	10	Sept. 25	10	n	Sept. 9	10	Sept. 25	10
O[6]	Sept. 26	10	Oct. 8	10	o[6]	Sept. 26	10	Oct. 9	10
P	Oct. 16	7	Oct. 29	6	p	Oct. 22	9	Nov. 8	8
Q	Oct. 31	9	Nov. 18	9	q	Nov. 9	10	Dec. 2	9
R	Nov. 20	10	Dec. 10	10	r	Nov. 20	8	Dec. 10	8
			1908.					1908.	
S	Dec. 12	10	Jan. 7	10	s	Dec. 12	10	Jan. 7	10
	1908.					1908.			
T	Jan. 7	10	Jan. 25	10	t	Jan. 7	10	Jan. 25	10.
U	Jan. 25	10	Feb. 15	4	u	Jan. 25	10	Feb. 15	9
V	Feb. 15	5	Mar. 3	5	v	Feb. 15	10	Mar. 3	7
W	Mar. 3	10	Mar. 19	10	w	Mar. 3	10	Mar. 19	10
X	Mar. 28	10	Apr. 13	5	x	Mar. 28	10	Apr. 13	6
Y	Apr. 13	10	Apr. 28	10	y	Apr. 13	10	Apr. 28	10
Z	Apr. 28	10	May 13	10	z	Apr. 28	10	May 13	10
AA	May 13	10	May 26	10	aa	May 13	10	May 26	10
BB	May 26	10	June 12	7	bb	May 26	7	June 12	7
CC	June 12	10	June 25	10	cc	June 12	10	June 25	10
DD	June 25	10	July 10	9	dd	June 25	10	July 10	10
EE	July 10	10	July 28	10	ee	July 10	10	July 28	7
FF	July 28	10	Aug. 12	[7] 5	ff	July 28	7		
GG	Aug. 12	10	Sept. 1	6					
HH	Sept. 1	10	Sept. 17	[8]					
II	Sept. 17	10	Oct. 2	10	ii[9]	Sept. 17	10	Oct. 2	10
JJ	Oct. 2	10	Oct. 22	10	jj	Oct. 2	10	Oct. 22	10
KK	Oct. 22	10	Nov. 6	10	kk	Oct. 22	10	Nov. 6	10
LL	Nov. 6	10	Nov. 20	6	ll	Nov. 6	10	Nov. 20	10
MM	Nov. 20	10	Dec. 12	9	mm	Nov. 20	10	Dec. 12	10
			1909.					1909.	
NN	Dec. 12	10	Jan. 10	9	nn	Dec. 12	10	Jan. 10	10
	1909.					1909.			
OO	Jan. 10	10	Feb. 7	2	oo	Jan. 10	10	Feb. 7	5
PP	Feb. 7	8	Feb. 23	8	pp	Feb. 7	10	Feb. 23	10
QQ	Feb. 23	9	Mar. 14	9	qq	Feb. 23	10	Mar. 14	10
RR	Mar. 14	10	Mar. 30	10	rr	Mar. 14	10	Mar. 30	10
SS	Mar. 30	10	Apr. 12	7	ss	Mar. 30	10	Apr. 12	6
TT	Apr. 14	10	Apr. 27	10	tt	Apr. 14	10	Apr. 27	10
UU	Apr. 27	4	May 20	4	uu	Apr. 27	5	May 20	5
VV	May 20	10	June 14	10	vv	May 20	10	June 14	10
WW	June 14	10	June 26	10	ww	June 14	10	June 26	10
XX	June 26	10	July 7	9	xx	June 26	10	July 7	9
YY	July 7	10	July 21	10	yy	July 7	10	July 21	10
ZZ	July 21	10	Aug. 2	10	zz	July 21	10	Aug. 2	10
AAA	Aug. 2	10	[10]	[10]	aaa	Aug 2	10	[10]	[10]

[1] Pustules vigorous.
[2] Series sent from Washington, D. C., to Minneapolis, Minn.
[3] Inoculations made from material from dried leaves.
[4] Three leaves inoculated from dried material, two from fresh.
[5] Plus sign signifies "more than"; i. e., exact number of leaves pustuled not noted.
[6] Series sent from Minneapolis, Minn., to Washington, D. C.
[7] Greenhouse excessively hot.
[8] Several.
[9] Inoculated from HH.
[10] Experiment discontinued.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA GRAMINIS AVENAE ON OATS.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[1] 9	a	Feb. 6	10	Feb. 19	[1] 4
B	Feb. 19	9	Mar. 5	[2] 0	b	Feb. 19	10	Mar. 5	[1] 2
C	Mar. 5	10	Mar. 25	[3] 9	c	Mar. 5	10	Mar. 25	[4] 9
D[5]	Mar. 25	10	Apr. 4	9	d[5]	Mar. 25	8	Apr. 4	7
E	Apr. 17	10	May 7	[6] 10	e	Apr. 17	10	May 7	[6] 9
F	May 8	10	May 26	10	f	May 8	10	May 26	10
G	May 27	10	June 10	10	g	May 27	10	June 10	10
H	June 11	10	June 23	10	h	June 11	10	June 23	10
I	June 24	10	July 8	10	i	June 24	10	July 8	10
J	July 8	10	July 21	[7] 4	j	July 8	10	July 21	10
K	July 22	10	Aug. 6	[8] 10	k	July 22	10	Aug. 6	10
L	Aug. 7	10	Aug. 21	10	l	Aug. 7	10	Aug. 21	10
M	Aug. 22	10	Sept. 8	10	m	Aug. 22	10	Sept. 8	10
N	Sept. 9	10	Sept. 25	10	n	Sept. 9	10	Sept. 25	10
O[9]	Sept. 26	10	Oct. 8	([10])	o[9]	Sept. 26	10	Oct. 8	([10])
P	Oct. 17	10	Oct. 29	10	p	Oct. 17	10	Oct. 29	10
Q	Oct. 31	10	Nov. 18	10	q	Oct. 31	10	Nov. 18	10
R	Nov. 20	10	Dec. 10	9	r	Nov. 20	8	Dec. 10	8
			1908.					1908.	
S	Dec. 12	10	Jan. 7	10	s	Dec. 12	10	Jan. 7	10
	1908.					1908.			
T	Jan. 7	10	Jan. 25	10	t	Jan. 7	10	Jan. 25	10
U	Jan. 25	10	Feb. 15	10	u	Jan. 25	10	Feb. 15	10
V	Feb. 15	10	Mar. 3	10	v	Feb. 15	10	Mar. 3	10
W[11]	Mar. 3	10	Mar. 19	10	w[11]	Mar. 3	10	Mar. 19	10
X	Mar. 30	10	Apr. 12	10	x	Mar. 30	10	Apr. 12	10
Y	Apr. 12	10	Apr. 28	10	y	Apr. 12	10	Apr. 28	10
Z	Apr. 28	10	May 13	10	z	Apr. 28	10	May 13	10
AA	May 13	10	May 26	10	aa	May 13	10	May 26	10
BB	May 26	10	June 12	10	bb	May 26	10	June 12	10
CC	June 12	10	June 25	10	cc	June 12	10	June 25	10
DD	June 25	10	July 10	10	dd	June 25	10	July 10	10
EE	July 10	10	July 28	10	ee	July 10	10	July 28	10
FF	July 28	9	Aug. 12	[12] 0	ff	July 28	10	Aug. 12	[13] 0
GG	Aug. 13	[14] 4	.....	.....	gg	Aug. 12	4	Sept. 1	3
.....	.....	.....	.....	.....	gg	Sept. 1	8	Sept. 17	([15])
HH	Sept. 17	10	Oct. 2	[16] 10	hh	Sept. 17	10	Oct. 2	10
II	Oct. 2	10	Oct. 22	10	ii	Oct. 2	10	Oct. 22	10
JJ	Oct. 22	10	Nov. 6	10	jj	Oct. 22	10	Nov. 6	9
KK	Nov. 6	10	Nov. 20	9	kk	Nov. 6	10	Nov. 20	9
LL	Nov. 20	10	Dec. 12	9	ll	Nov. 20	10	Dec. 12	9
			1909.					1909.	
MM	Dec. 12	10	Jan. 10	9	mm	Dec. 12	10	Jan. 10	8
	1909.					1909.			
NN	Jan. 10	9	Feb. 7	5	nn	Jan. 10	10	Feb. 7	4
OO	Feb. 7	10	Feb. 23	10	oo	Feb. 7	10	Feb. 23	10
PP	Feb. 23	10	Mar. 14	10	pp	Feb. 23	10	Mar. 14	10
QQ	Mar. 14	10	Mar. 30	10	q	Mar. 14	10	Mar. 30	10
RR	Mar. 30	10	Apr. 12	8	rr	Mar. 30	10	Apr. 12	5
SS	Apr. 12	10	Apr. 27	10	ss	Apr. 12	10	Apr. 27	10
TT	Apr. 27	9	May 20	9	tt	Apr. 27	9	May 20	9
UU	May 20	10	June 14	10	uu	May 20	10	June 14	10
VV	June 14	10	June 26	10	vv	June 14	10	June 26	10
WW	June 26	10	July 7	10	ww	June 26	10	July 7	10
XX	July 7	10	July 21	10	xx	July 7	10	July 21	10
YY	July 21	10	([17])	([17])	yy	July 21	10	([17])	([17])

[1] Pustules vigorous.
[2] Accidental infection by *Puccinia coronata;* plants discarded.
[3] Slightly mixed with *Puccini coronata.*
[4] Mixed with *Puccinia coronata.*
[5] Series sent from Washington, D. C., to Minneapolis, Minn., April 8, 1907.
[6] Inoculations made from material from dried leaves.
[7] Badly mixed with *Puccinia coronata.*
[8] Inoculations made from J.
[9] Series sent from Minneapolis, Minn., to Washington, D. C., October 8, 1907.
[10] Several.
[11] Series sent from Washington, D. C., to Minneapolis, Minn., March 19, 1908.
[12] Failure due to extreme heat in greenhouse.
[13] Five leaves pustuled with *Puccinia coronata,* accidental infection. Failure of *Puccinia graminis* due to extreme heat in greenhouse.
[14] Inoculated from EE.
[15] Not recorded.
[16] Inoculated from gg.
[17] Experiment discontinued.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA GRAMINIS HORDEI ON BARLEY.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[1] 7	a	Feb. 6	10	Feb. 19	8
B	Feb. 19	10	Mar. 5	10	b	Feb. 19	10	Mar. 5	8
C	Mar. 5	10	Mar. 25	10	c	Mar. 5	10	Mar. 25	10
D[2]	Mar. 25	7	Apr. 4	6	d[2]	Mar. 25	10	Apr. 4	10
E	Apr. 17	[3] 10	May 7	7	e	Apr. 17	7	May 7	8
F	May 7	10	May 25	10	f	May 7	10	May 25	10
G	May 26	8	June 13	[4]+5	g	May 26	8	June 13	[4]+5
H	June 14	10	June 25	[4]+5	h	June 14	10	June 25	[4]+5
I	June 26	10	July 9	[5] 2	i	June 26	9	July 9	[6] 8
J	July 10	5	July 21	3	j	July 10	9	July 21	7
K	July 22	10	Aug. 6	10	k	July 22	10	Aug. 6	10
L	Aug. 7	10	Aug. 21	10	l	Aug. 7	10	Aug. 21	10
M	Aug. 22	10	Sept. 8	10	m	Aug. 22	10	Sept. 8	10
N	Sept. 9	10	Sept. 25	10	n	Sept. 9	10	Sept. 25	10
O[7]	Sept. 26	10	Oct. 8	([8])	o[7]	Sept. 26	10	Oct. 8	([8])
P	Oct. 22	11	Nov. 8	11	p	Oct. 16	9	Oct. 29	9
Q	Nov. 9	10	Nov. 20	10	q	Oct. 31	7	Nov. 18	7
R	Nov. 20	9	Dec. 10	5	r	Nov. 20	9	Dec. 10	8
			1908.					1908.	
S	Dec. 12	10	Jan. 7	10	s	Dec. 12	10	Jan. 7	10
	1908.					1908.			
T	Jan. 7	10	Jan. 25	[9] 10	t	Jan. 7	10	Jan. 25	[10] 10
U	Jan. 25	10	Feb. 15	[10] 8	u	Jan. 25	10	Feb. 15	9
V	Feb. 15	10	Mar. 3	10	v	Feb. 15	10	Mar. 3	10
W[11]	Mar. 3	10	Mar. 19	10	w[11]	Mar. 3	10	Mar. 19	10
X	Mar. 27	10	Apr. 13	7	x	Mar. 27	10	Apr. 13	6
Y	Apr. 13	10	Apr. 28	4	y	Apr. 13	10	Apr. 28	3
Z	Apr. 28	10	May 13	10	z	Apr. 28	10	May 13	5
AA	May 13	10	May 26	8	aa	May 13	6	May 26	5
BB	May 26	10	June 12	8	bb	May 26	10	June 12	5
CC	June 18	10	July 10	[12] 0	cc	June 18	10	July 10	1
					dd	July 10	7	July 28	3
					ee	July 28	7	Aug. 12	1
					ff	Aug. 12	10	Sept. 1	8
					gg	Sept. 1	10	Sept. 17	([8])
HH	Sept. 17	10	Oct. 2	[13] 10	hh	Sept. 17	10	Oct. 2	8
II	Oct. 2	10	Oct. 22	10	ii	Oct. 2	10	Oct. 22	10
JJ	Oct. 22	10	Nov. 6	10	jj	Oct. 22	10	Nov. 6	10
KK	Nov. 6	10	Nov. 20	10	kk	Nov. 6	10	Nov. 20	10
LL	Nov. 20	10	Dec. 12	8	ll	Nov. 20	10	Dec. 12	8
			1909.					1909.	
MM	Dec. 12	10	Jan. 10	9	mm	Dec. 12	8	Jan. 10	5
	1909.					1909.			
NN	Jan. 10	5	Feb. 7	1	nn	Jan. 10	10	Feb. 7	3
OO	Feb. 22	5	Mar. 14	3	oo	Feb. 22	6	Mar. 14	2
PP	Mar. 14	10	Mar. 30	10	pp	Mar. 14	10	Mar. 30	10
QQ	Mar. 30	10	Apr. 12	9	qq	Mar. 30	10	Apr. 14	6
RR	Apr. 12	10	Apr. 27	10	rr	Apr. 12	10	Apr. 27	10
SS	Apr. 27	10	May 20	7	ss	Apr. 27	4	May 20	4
TT	May 20	8	June 14	7	tt	May 20	10	June 14	9
UU	June 14	10	June 26	8	uu	June 14	10	June 26	8
VV	June 26	10	July 7	10	vv	June 26	10	July 7	10
WW	July 7	10	July 21	7	ww	July 7	10	July 21	10
XX	July 21	10	Aug. 2	10	xx	July 21	10	Aug. 2	10
YY	Aug. 2	10	([14])	([14])	yy	Aug. 2	10	([14])	([14])

[1] Pustules vigorous.
[2] Series sent from Washington, D. C., to Minneapolis, Minn., April 8, 1907.
[3] Three inoculations were made from material from dried leaves, 7 from fresh material shipped in pots.
[4] Plus sign signifies "more than;" i. e., exact number of leaves pustuled not noted.
[5] Slugs destroyed 8 plants.
[6] Slugs destroyed 1 plant.
[7] Series sent from Minneapolis, Minn., to Washington, D. C., October 8, 1907.
[8] Several.
[9] Pustules not as vigorous as usual.
[10] Pustules not vigorous.
[11] Series transferred from Washington, D. C., to Minneapolis, Minn., March 19, 1908.
[12] Failure due to extreme heat in greenhouse.
[13] Inoculated from gg.
[14] Experiment discontinued.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA GRAMINIS SECALIS ON RYE.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[1] 7	a	Feb. 6	10	Feb. 19	4
B	Feb. 19	10	Mar. 5	4	b	Feb. 19	10	Mar. 5	4
C	Mar. 5	10	Mar. 25	8	c	Mar. 5	10	Mar. 25	5
D[2]	Apr. 4	4	Apr. 8	8	d[2]	Mar. 25	5	Apr. 8	3
E	Apr. 17	10	May 7	4	e	Apr. 17	[3] 9	May 7	2
F	May 8	6	May 26	([4])	f	May 8	10	May 26	([4])
G	May 27	5	June 13	([4])	g	May 27	6	June 13	([4])
H	June 14	4	June 26	[5] 0	h	June 14	9	June 26	[5] 0
	1909.		1909.			1909.		1909.	
AA[6]	July 7	10	July 21	10	aa[6]	July 7	10	July 21	10
BB	July 21	10	Aug. 2	8	bb	July 21	10	Aug. 2	8
CC	Aug. 2	10		([7])	cc	Aug. 2	10		([7])

PUCCINIA RUBIGO-VERA TRITICI ON WHEAT.

	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[1] 7	a	Feb. 6	10	Feb. 19	[1] 10
B	Feb. 19	10	Mar. 5	8	b	Feb. 19	10	Mar. 5	[1] 8
C	Mar. 5	10	Mar. 21	([4])	c	Mar. 5	10	Mar. 21	([4])
D[2]	Mar. 26	10	Apr. 8	0	d[2]	Mar. 26	10	Apr. 8	7
E[8]	Apr. 17				e	Apr. 17	[3] 7	May 7	7
F					f	May 8	10	May 28	[9] +5
G					g	May 29	9	June 13	[9] +5
H					h	June 14	10	June 26	[9] +5
I					i	June 27	10	July 9	3
J					j	July 10	10	July 23	10
K	July 24	10	Aug. 8	[10] 7	k	July 24	10	Aug. 8	10
L	Aug. 9	8	Aug. 21	0	l	Aug. 9	10	Aug. 21	0
L	Aug. 22	[11] 6	Sept. 10	5	l	Aug. 22	[11] 6	Sept. 10	5
M	Sept. 11	5	Sept. 27	5	m	Sept. 11	9	Sept. 27	9
N[12]	Sept. 28	9	Oct. 8	([4])	n[12]	Sept. 28	10	Oct. 8	([4])
O	Oct. 24	8	Nov. 8	3	o	Oct. 16	8	Oct. 29	8
P	Nov. 9	7	Nov. 20	7	p	Oct. 31	10	Nov. 18	10
Q	Nov. 20	9	Dec. 10	9	q	Nov. 20	10	Dec. 10	10
			1908.					1908.	
R	Dec. 12	10	Jan. 7	10	r	Dec. 12	10	Jan. 7	10
	1908.					1908.			
S	Jan. 7	10	Jan. 25	10	s	Jan. 7	10	Jan. 25	10
T	Jan. 25	10	Feb. 15	10	t	Jan. 25	10	Feb. 15	10
U	Feb. 15	10	Mar. 3	10	u	Feb. 15	10	Mar. 3	10
V[13]	Mar. 3	10	Mar. 19	10	v[13]	Mar. 3	10	Mar. 19	10
W	Mar. 30	10	Apr. 13	10	w	Mar. 30	10	Apr. 13	10
X	Apr. 13	10	Apr. 28	7	x	Apr. 13	10	Apr. 28	10
Y	Apr. 28	10	May 13	10	y	Apr. 28	10	May 13	10
Z	May 13	10	May 26	10	z	May 13	10	May 26	10
AA	May 26	10	June 12	10	aa	May 26	10	June 12	10
BB	June 12	10	June 25	10	bb	June 12	10	June 25	10
CC	June 25	10	July 10	10	cc	June 25	7	July 10	7
DD	July 10	10	July 28	8	dd	July 10	10	July 28	10
EE	July 28	6	Aug. 12	2	ee	July 28	10	Aug. 12	5
FF	Aug. 12	5	Sept. 1	1	ff	Aug. 12	10	Sept. 1	7
GG[14]	Sept. 1	3	Sept. 17	([4])	gg[14]	Sept. 1	9	Sept. 17	([4])

[1] Pustules vigorous.
[2] Series sent from Washington, D. C., to Minneapolis, Minn., April 8, 1907.
[3] Inoculations made from material from dried leaves.
[4] Several.
[5] Very hot when inoculations were made, hence no infection.
[6] Not successive to preceding inoculations; material obtained directly from the field.
[7] Failure due to extreme heat in greenhouse.
[8] Material from D destroyed in transit.
[9] Plus sign signifies "more than;" i. e., exact number of leaves pustuled not noted.
[10] Inoculations made from j.
[11] Inoculations made from K and k.
[12] Series sent from Minneapolis, Minn., to Washington, D. C., October 8, 1907.
[13] Series sent from Washington, D. C., to Minneapolis, Minn., March 19, 1908.
[14] Letters HH and hh were omitted in the series.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA RUBIGO-VERA TRITICI ON WHEAT—Continued.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1908.		1908.			1908.		1908.	
II	Sept. 17	8	Oct. 2	8	ii	Sept. 17	10	Oct. 2	10
JJ	Oct. 2	10	Oct. 22	10	jj	Oct. 2	10	Oct. 22	10
KK	Oct. 22	10	Nov. 6	9	kk	Oct. 22	10	Nov. 6	8
LL	Nov. 6	10	Nov. 20	10	ll	Nov. 6	10	Nov. 20	10
MM	Nov. 20	9	Dec. 12	9	mm	Nov. 20	10	Dec. 12	10
			1909.					1909.	
NN	Dec. 12	10	Jan. 10	10	nn	Dec. 12	10	Jan. 10	7
	1909.					1909.			
OO	Jan. 10	10	Feb. 7	5	oo	Jan. 10	10	Feb. 7	2
PP	Feb. 7	7	Feb. 23	7	pp	Feb. 7	5	Feb. 23	5
QQ	Feb. 23	10	Mar. 14	10	qq	Feb. 23	10	Mar. 14	10
RR	Mar. 14	10	Mar. 30	10	rr	Mar. 14	10	Mar. 30	10
SS	Mar. 30	10	Apr. 12	7	ss	Mar. 30	10	Apr. 12	1
TT	Apr. 12	10	Apr. 27	2	tt	Apr. 12	10	Apr. 27	2
UU	Apr. 27	3	May 20	3	uu	Apr. 27	5	May 20	5
VV	May 20	10	June 14	10	vv	May 20	10	June 14	9
WW	June 14	8	June 26	7	ww	June 14	10	June 26	9
XX	June 26	10	July 7	7	xx	June 26	10	July 7	10
YY	July 7	10	July 21	8	yy	July 7	10	July 21	10
ZZ	July 31	10	Aug. 2	10	zz	July 21	10	Aug. 2	10
AAA	Aug. 2	10	[1]	[1]	aaa	Aug. 2	10	[1]	[1]

PUCCINIA SIMPLEX ON BARLEY.

	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	10	a	Feb. 6	10	Feb. 19	10
B	Feb. 19	10	Mar. 5	10	b	Feb. 19	10	Mar. 5	10
C	Mar. 5	10	Mar. 26	[2]	c	Mar. 5	10	Mar. 26	[2]
D [3]	Mar. 26	10	Apr. 4	10	d [3]	Mar. 26	10	Apr. 4	8
E	Apr. 17	[4] 7	May 7	7	e	Apr. 17	[4] 9	May 7	7
F	May 8	10	May 28	10	f	May 8	10	May 28	10
G	May 29	10	June 13	10	g	May 29	10	June 13	10
H	June 14	10	June 25	10	h	June 14	10	June 25	[2]
I	June 26	10	July 8	10	i	June 26	10	July 8	10
J	July 10	10	July 23	10	j	July 10	10	July 23	10
K	July 24	10	Aug. 7	10	k	July 24	10	Aug. 7	10
L	Aug. 9	10	Aug. 23	10	l	Aug. 9	10	Aug. 23	10
M	Aug. 24	10	Sept. 8	10	m	Aug. 24	10	Sept. 8	10
N	Sept. 9	10	Sept. 27	10	n	Sept. 9	10	Sept. 27	10
O [5]	Sept. 28	10	Oct. 8	[2]	o [5]	Sept. 28	10	Oct. 8	[2]
P	Oct. 24	10	Nov. 8	7	p	Oct. 16	10	Oct. 29	10
Q	Nov. 9	9	Nov. 18	9	q	Oct. 31	10	Nov. 18	10
R	Nov. 20	10	Dec. 10	10	r	Nov. 20	10	Dec. 10	10
			1908.					1908.	
S	Dec. 12	10	Jan. 7	10	s	Dec. 12	10	Jan. 7	10
	1908.					1908.			
T	Jan. 7	10	Jan. 25	10	t	Jan. 7	10	Jan. 25	10
U	Jan. 25	10	Feb. 15	10	u	Jan. 25	10	Feb. 15	10
V	Feb. 15	10	Mar. 3	10	v	Feb. 15	10	Mar. 3	10
W [3]	Mar. 3	10	Mar. 19	10	w [3]	Mar. 3	10	Mar. 19	10
X	Mar. 30	10	Apr. 13	10	x	Apr. 2	10	Apr. 13	10
Y	Apr. 13	10	Apr. 28	10	y	Apr. 13	8	Apr. 28	8
Z	Apr. 28	10	May 13	10	z	Apr. 28	10	May 13	10
AA	May 13	10	May 26	10	aa	May 13	10	May 26	10
BB	May 26	10	June 12	10	bb	May 26	10	June 12	10
CC	June 12	10	June 25	10	cc	June 12	10	June 25	10
DD	June 25	10	July 10	10	dd	June 25	10	July 10	10
EE	July 10	10	July 28	10	ee	July 10	10	July 28	10
FF	July 28	9	Aug. 12	[6] 2	ff	July 28	10	Aug. 12	[6] 3
GG	Aug. 12	4	Sept. 1	4	gg	Aug. 12	1	Sept. 1	1
HH	Sept. 1	10	Sept. 17	[7]	hh	Sept. 1	8	Sept. 17	

[1] Experiments discontinued.
[2] Several.
[3] Series sent from Washington, D. C., to Minneapolis, Minn.
[4] Inoculations made from material from dried leaves.
[5] Series sent from Minneapolis, Minn., to Washington, D. C., October 8, 1907.
[6] Extreme heat in greenhouse.
[7] Not recorded.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA SIMPLEX ON BARLEY—Continued.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled
	1908.		1908.			1908.		1908.	
II	Sept. 17	6	Oct. 2	4	ii	Sept. 17	7	Oct. 2	4
JJ	Oct. 2	10	Oct. 22	10	jj	Oct. 2	10	Oct. 22	10
KK	Oct. 22	10	Nov. 6	10	kk	Oct. 22	10	Nov. 6	10
LL	Nov. 6	10	Nov. 20	9	ll	Nov. 6	10	Nov. 20	10
MM	Nov. 20	9	Dec. 12	8	mm	Nov. 20	10	Dec. 12	9
			1909.					1909.	
NN	Dec. 12	7	Jan. 10	7	nn	Dec. 12	10	Jan. 10	9
	1909.					1909.			
OO	Jan. 10	8	Feb. 7	4	oo	Jan. 10	10	Feb. 7	7
PP	Feb. 7	10	Feb. 23	10	pp	Feb. 7	10	Feb. 23	10
QQ	Feb. 23	10	Mar. 14	10	qq	Feb. 23	10	Mar. 14	10
RR	Mar. 14	10	Mar. 30	10	rr	Mar. 14	10	Mar. 30	10
SS	Mar. 30	10	Apr. 12	8	ss	Mar. 30	10	Apr. 12	6
TT	Apr. 12	10	Apr. 27	10	tt	Apr. 12	10	Apr. 27	10
UU	Apr. 27	4	May 20	4	uu	Apr. 27	7	May 20	7
VV	May 20	10	June 14	10	vv	May 20	10	June 14	10
WW	June 14	10	June 26	10	ww	June 14	10	June 26	10
XX	June 26	10	July 7	0	xx	June 26	10	July 7	4
XX	July 7	10	July 21	10	yy	July 7	10	July 21	9
YY	July 21	10	Aug. 2	10	zz	July 21	10	Aug. 2	10
ZZ	Aug. 2	10	[1]	[1]	aaa	Aug. 2	8	[1]	[1]

PUCCINIA CORONATA ON OATS.

	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[2] 9	a	Feb. 6	10	Feb. 19	10
B	Feb. 19	9	Mar. 5	9	b	Feb. 19	10	Mar. 5	10
C	Mar. 5	9	Mar. 21	9	c	Mar. 5	10	Mar. 21	10
D [3]	Mar. 21	10	Mar. 30	10	d [3]	Mar. 21	10	Mar. 30	10
E	Apr. 17	[4] 10	May 7	10	e	Apr. 17	[4] 10	May 7	10
F	May 8	10	May 26	10	f	May 8	10	May 26	10
G	May 27	8	June 10	8	g	May 27	9	June 10	9
H	June 11	10	June 23	10	h	June 11	10	June 23	10
I	June 24	10	July 8	10	i	June 24	10	July 8	10
J	July 8	10	July 23	10	j	July 8	10	July 23	10
K	July 24	10	Aug. 8	10	k	July 24	10	Aug. 8	10
L	Aug. 9	10	Aug. 23	10	l	Aug. 9	10	Aug. 23	10
M	Aug. 24	10	Sept. 10	10	m	Aug. 24	10	Sept. 10	10
N	Sept. 11	10	Sept. 27	10	n	Sept. 11	10	Sept. 27	10
O [5]	Sept. 28	10	Oct. 8	[6]	o [5]	Sept. 28	10	Oct. 8	[6]
P	Oct. 24	9	Nov. 8	8	p	Oct. 17	10	Oct. 29	10
Q	Nov. 9	10	Nov. 18	10	q	Oct. 31	10	Nov. 18	10
R	Nov. 20	9	Dec. 10	9	r	Nov. 20	8	Dec. 10	8
			1908.					1908.	
S	Dec. 12	10	Jan. 7	10	s	Dec. 12	10	Jan. 7	10
	1908.					1908.			
T	Jan. 7	10	Jan. 25	10	t	Jan. 7	10	Jan. 25	10
U	Jan. 25	10	Feb. 15	10	u	Jan. 25	10	Feb. 15	10
V	Feb. 15	10	Mar. 3	10	v	Feb. 15	10	Mar. 3	10
W [3]	Mar. 3	10	Mar. 19	10	w [3]	Mar. 3	10	Mar. 19	10
X	Mar. 30	10	Apr. 13	10	x	Mar. 30	10	Apr. 13	10
Y	Apr. 13	10	Apr. 28	10	y	Apr. 13	10	Apr. 28	10
Z	Apr. 28	10	May 13	10	z	Apr. 28	10	May 13	10
AA	May 13	10	May 26	10	aa	May 13	10	May 26	10
BB	May 26	10	June 12	10	bb	May 26	10	June 12	10
CC	June 12	10	June 25	10	cc	June 12	10	June 25	10
DD	June 25	10	July 10	10	dd	June 25	10	July 10	10
EE	July 10	10	July 28	10	ee	July 10	10	July 28	10
FF	July 28	9	Aug. 12	8	ff	July 28	9	Aug. 12	8
GG	Aug. 13	10	Sept. 1	10	gg	Aug. 13	10	Sept. 1	10

[1] Experiments discontinued.
[2] Pustules vigorous.
[3] Series sent from Washington, D. C., to Minneapolis, Minn.
[4] Inoculations made from material from dried leaves.
[5] Series sent from Minneapolis, Minn., to Washington, D. C.
[6] Several.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA CORONATA ON OATS—Continued.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1908.		1908.			1908.		1908.	
HH	Sept. 1	10	Sept. 17	(1)	hh	Sept. 1	10	Sept. 17	(1)
II	Sept. 17	10	Oct. 2	8	ii	Sept. 17	10	Oct. 2	8
JJ	Oct. 2	10	Oct. 22	10	jj	Oct. 2	10	Oct. 22	10
KK	Oct. 22	10	Nov. 6	10	kk	Oct. 22	10	Nov. 6	10
LL	Nov. 6	10	Nov. 20	9	ll	Nov. 6	10	Nov. 20	10
MM	Nov. 20	10	Dec. 12	10	mm	Nov. 20	10	Dec. 12	10
	1909.		1909.			1909.		1909.	
NN	Dec. 12	10	Jan. 10	8	nn	Dec. 12	9	Jan. 10	9
	1909.					1909.			
OO	Jan. 10	10	Feb. 7	10	oo	Jan. 10	10	Feb. 7	5
PP	Feb. 7	10	Feb. 23	10	pp	Feb. 7	10	Feb. 23	10
QQ	Feb. 23	10	Mar. 14	10	qq	Feb. 23	10	Mar. 14	10
RR	Mar. 14	10	Mar. 30	10	rr	Mar. 14	10	Mar. 30	10
SS	Mar. 30	10	Apr. 12	8	ss	Mar. 30	10	Apr. 12	6
TT	Apr. 12	10	Apr. 27	10	tt	Apr. 12	10	Apr. 27	10
UU	Apr. 27	7	May 20	7	uu	Apr. 27	9	May 20	9
VV	May 20	10	June 14	10	vv	May 20	10	June 14	10
WW	June 14	10	June 26	10	ww	June 14	10	June 26	10
XX	June 26	10	July 7	9	xx	June 26	10	July 7	10
YY	July 7	10	July 21	10	yy	July 7	10	July 21	10
ZZ	July 21	10	Aug. 2	10	zz	July 21	10	Aug. 2	10
AAA	Aug. 2	10	(2)	(2)	aaa	Aug. 2	10	(2)	(2)

PUCCINIA RUBIGO-VERA SECALIS ON RYE.

	1907.		1907.			1907.		1907.	
A	Feb. 6	10	Feb. 19	[3] 9	a	Feb. 6	10	Feb. 19	[3] 10
B	Feb. 19	10	Mar. 5	9	b	Feb. 19	10	Mar. 5	8
C	Mar. 5	10	Mar. 27	3	c	Mar. 5	10	Mar. 25	(4)
D[9]	Mar. 27	3	Apr. 8	1	d[9]	Mar. 27	3	Apr. 8	1
E[6]	Apr. 17				e	Apr. 17	[7] 2	May 7	1
F					f	May 8	10	May 26	(4)
G					g	May 27	10	June 10	(4)
H					h	June 11	10	June 25	(4)
I					i	June 26	10	July 8	7
J					j	July 10	10	July 23	10
K					k	July 24	10	Aug. 8	10
L					l	Aug. 9	10	Aug. 23	2
M					m	Aug. 24	10	Sept. 10	10
N	Sept. 11	10	Sept. 27	[3] 10	n	Sept. 11	10	Sept. 27	10
O[9]	Sept. 28	10	Oct. 8	(4)	o[9]	Sept. 28	10	Oct. 8	(4)
P	Oct. 16	6	Oct. 29	6	p	Oct. 16	5	Oct. 31	5
Q	Oct. 31	10	Nov. 18	9	q	Oct. 31	9	Nov. 18	9
R	Nov. 20	10	Dec. 10	10	r	Nov. 20	10	Dec. 10	10
			1908.					1908.	
S	Dec. 12	8	Jan. 7	8	s	Dec. 12	10	Jan. 7	10
	1908.					1908.			
T	Jan. 7	9	Jan. 25	10	t	Jan. 7	9	Jan. 25	10
U	Jan. 25	10	Feb. 15	10	u	Jan. 25	10	Feb. 15	10
V	Feb. 15	10	Mar. 3	10	v	Feb. 15	10	Mar. 3	10
W[5]	Mar. 3	10	Mar. 19	10	w[5]	Mar. 3	10	Mar. 19	10
X	Mar. 30	10	Apr. 13	10	x	Mar. 30	10	Apr. 13	10
Y	Apr. 13	10	Apr. 28	10	y	Apr. 13	10	Apr. 28	10
Z	Apr. 28	10	May 13	10	z	Apr. 28	10	May 13	10
AA	May 13	10	May 26	10	aa	May 13	10	May 26	10
BB	May 26	10	June 12	10	bb	May 26	10	June 12	10
CC	June 12	9	June 25	9	cc	June 12	10	June 25	10
DD	June 25	7	July 10	5	dd	June 25	10	July 10	10

[1] Not recorded.
[2] Experiments discontinued.
[3] Pustules vigorous.
[4] Several.
[5] Series sent from Washington, D. C., to Minneapolis, Minn.
[6] Lost in transit.
[7] Inoculations made from material from dried leaves.
[8] Inoculations made from m.
[9] Series sent from Minneapolis, Minn., to Washington, D. C.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA RUBIGO-VERA SECALIS ON RYE—Continued.

Capital letter series.					Lower-case letter series.				
Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Series letter.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
	1908.		1908.			1908.		1908.	
EE	July 10	6	July 28	6	ee	July 10	4	July 28	4
FF	July 28	9	Aug. 12	[1] 1	ff	July 28	6	Aug. 12	[1] 0
GG	Aug. 13	8	Sept. 1	5	gg				
HH	Sept. 1	10	Sept. 17	[2]	hh	Sept. 1	[3] 9	Sept. 17	[2]
II	Sept. 17	10	Oct. 2	10	ii	Sept. 17	10	Oct. 2	10
JJ	Oct. 2	10	Oct. 22	10	jj	Oct. 2	10	Oct. 22	10
KK	Oct. 22	10	Nov. 6	10	kk	Oct. 22	10	Nov. 6	10
LL	Nov. 6	8	Nov. 20	8	ll	Nov. 6	10	Nov. 20	10
MM	Nov. 20	7	Dec. 12	4	mm	Nov. 20	9	Dec. 12	9
			1909.					1909.	
NN	Sec. 12	10	Jan. 10	8	nn	Dec. 12	10	Jan. 10	10
	1909.					1909.			
OO	Jan. 10	7	Feb. 7	4	oo	Jan. 10	10	Feb. 7	5
PP	Feb. 7	10	Feb. 23	10	pp	Feb. 7	8	Feb. 23	8
QQ	Feb. 23	10	Mar. 14	10	qq	Feb. 23	10	Mar. 14	10
RR	Mar. 14	10	Mar. 30	10	rr	Mar. 14	10	Mar. 30	10
SS	Mar. 30	10	Apr. 12	10	ss	Mar. 30	10	Apr. 12	10
TT	Apr. 12	10	Apr. 27	10	tt	Apr. 12	10	Apr. 27	10
UU	Apr 27	10	May 20	10	uu	Apr. 27	10	May 20	10
VV	May 20	10	June 14	10	vv	May 20	10	June 14	10
WW	June 14	8	June 26	8	ww	June 14	8	June 26	8
XX	June 26	10	July 7	10	xx	June 26	10	July 7	10
YY	July 7	10	July 21	9	yy	July 7	10	July 21	8
ZZ	July 21	10	[4]	[4]	zz	July 21	8	[4]	[4]

PUCCINIA GRAMINIS TRITICI ON BARLEY FROM WHEAT.[5]

Original inoculation made Nov. 13, 1906.				Original inoculation made Nov. 22, 1906.			
Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
1907.		1907.		1907.		1907.	
Apr. 17	10	May 7	[6] 8	Apr. 17	10	May 7	[6] 10
May 7	10	May 29	10	May 8	10	May 26	10
May 29	10	June 11	10	May 27	10	June 11	10
June 11	10	June 26	10	June 11	10	June 26	10
June 26	10	July 8	6	June 26	10	July 8	10
July 8	10	July 21	6	July 8	10	July 21	10
July 22	9	Aug. 6	8	July 22	10	Aug. 6	10
Aug. 7	8	Aug. 21	8	Aug. 7	10	Aug. 21	10
Aug. 22	8	Sept. 8	8	Aug. 22	10	Sept. 8	10
Sept. 9	10	Sept. 25	10	Sept. 9	10	Sept. 25	10
Sept. 26	10	Oct. 8[7]	10				
Oct. 17	9	Oct. 29	9	Oct. 17	[6] 4	Oct. 29	3
Oct. 31	10	Nov. 18	10	Oct. 31	10	Nov. 18	10
Nov. 20	10	Dec. 10	10	Nov. 20	10	Dec. 10	10
		1908.				1908.	
Dec. 12	6	Jan. 8	6	Dec. 12	6	Jan 8	6
1908.				1908.			
Feb. 15	[9] 7	Mar. 3	7	Feb. 15	[9] 6	Mar. 3	6

[1] Extreme heat in greenhouse.
[2] Several.
[3] Inoculations made from GG.
[4] Experiments discontinued.
[5] The original material was obtained from wheat November 13 and 22, 1906. It was transferred to barley and was kept on barley continuously from that time. Notes on the inoculations from November 13 and 22, respectively, to March 30, 1907, have been mislaid or lost; but six series of successful inoculations were made in each case at Washington, D. C., and on March 30 the successfully inoculated plants were sent to Minnesota. The table gives the results from inoculations from this material, beginning with April 17, 1907.
[6] Pustules vigorous.
[7] Series sent from Minneapolis, Minn., to Washington, D. C., October, 8, 1907.
[8] Inoculations made from material pustuled September 25, 1907.
[9] Inoculations made from material pustuled January 8, 1908.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA GRAMINIS TRITICI ON BARLEY FROM WHEAT—Continued.

Original inoculation made Nov. 13, 1906.				Original inoculation made Nov. 22, 1906.			
Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
1908.		1908.		1908.		1908.	
Mar. 3	10	Mar. 19[1]	10	Mar. 3	10	Mar. 19	10
Mar. 30	10	Apr. 28	2	Mar. 30	10	Apr. 12	8
Apr. 28	10	May 13	10	Apr. 12	6	Apr. 28	6
May 13	10	May 26	10	Apr. 28	10	May 13	9
May 26	10	June 12	5				
June 12	10	July 10	2				
July 10	7	July 28	1	May 13	10	May 26	10
July 28	7	Aug. 12	[2] 1	May 26	10	June 12	2
Aug. 12	1	Sept. 1	1	June 12[3]			
Sept. 1	5	Sept. 17	5				
Sept. 17	9	Oct. 2	6				
Oct. 2	10	Oct. 24	10				
Oct. 24	10	Nov. 6	10				
Nov. 6	10	Nov. 20	10				
Nov. 20	10	Dec. 12	8				
		1909.					
Dec. 12	8	Jan. 10	8				
1909.							
Jan. 10	7	Feb. 7	2				
Feb. 7	7	Feb. 23	[4]				
Feb 23	16	Mar. 14	8				
Mar. 14	10	Mar. 30	10				
Mar. 30	10	Apr. 12	7				
Apr. 12	8	Apr. 27	7				
Apr. 27	6	May 20	6				
May 20	10	June 14	9				
June 14	10	June 26	10				
June 26	10	July 7	10				
July 7	10	July 21	10				
July 21	10	Aug. 2	10				
Aug. 2	10						

PUCCINIA GRAMINIS HORDEI ON WHEAT FROM BARLEY.[5]

Original inoculation made Nov. 14, 1906.				Original inoculation made Nov. 22, 1906.			
Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
1907.		1907.		1907.		1907.	
Apr. 17	8	May 7	7	Apr. 17	10	May 7	10
May 9	10	May 28	10	May 8	10	May 28	10
May 28	10	June 11	7	May 28	10	June 11	10
June 11	10	June 24	7	June 11	10	June 24	10
June 24	10	July 8	4	June 24	10	July 8	6
July 8	10	July 21	1	July 8	10	July 21	7
July 22	5	Aug. 6	2	July 22	10	Aug. 6	8
Aug. 6	8	Aug 21	8	Aug. 7	10	Aug. 21	10
Aug. 22	8	Sept. 8	8	Aug. 22	10	Sept. 8	10
Sept. 9	10	Sept. 25[6]	10	Sept. 9	10	Sept. 25	10
Oct. 17	9	Oct. 29	6	Oct. 16	9	Oct. 29	9

[1] Series sent from Washington, D. C., to Minneapolis, Minn.
[2] Extreme heat in greenhouse.
[3] Accidentally mixed with *Puccinia simplex;* discarded.
[4] Notes not taken.
[5] The original material was obtained from barley November 14 and November 22, 1906. It was transferred to wheat and was kept on wheat continuously from that time. Notes on the inoculations from November 14 and 22, respectively, to March 30, 1907, have been mislaid or lost; but six series of successful inoculations were made in each case at Washington, D. C., and on March 30 the successfully inoculated plants were sent to Minnesota. The table gives the results from inoculations from this material, beginning with April 17, 1907.
[6] Series sent from Minneapolis, Minn., to Washington, D. C., October 8, 1907.

TABLE III.—*Summary of experiments to determine the vitality of successive uredo generations of various grain rusts*—Continued.

PUCCINIA GRAMINIS HORDEI ON WHEAT FROM BARLEY—Continued.

Original inoculation made Nov. 14, 1906.				Original inoculation made Nov. 22, 1906.			
Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.	Date of inoculation.	Number of leaves inoculated.	Date matured.	Number of leaves pustuled.
1907.		1907.		1907.		1907.	
Oct. 31	8	Nov. 18	8	Oct. 31	9	Nov. 18	9
Nov. 20	10	Dec. 10	10	Nov. 20	10	Dec. 10	10
		1908.				1908.	
Dec. 12	10	Jan. 8	10	Dec. 12	10	Jan. 8	10
1908.				1908.			
Jan. 25	10	Feb. 15	4	Jan. 25	10	Feb. 15	10
Feb. 15	6	Mar. 3	6	Feb. 15	10	Mar. 3	6
Mar. 3	10	Mar. 19[1]	10	Mar. 3	10	Mar. 19[1]	10
Mar. 31	10	Apr. 13	9	Mar. 30	10	Apr. 13	9
Apr. 13	7	Apr. 27	7	Apr. 13	8	Apr. 27	8
Apr. 27	10	May 13	10	Apr. 27	10	May 13	10
May 13	10	May 26	10	May 13	10	May 26	10
May 26	10	June 12	10	May 26	10	June 12	10
June 12	10	June 25	10	June 12	10	June 25	10
June 25	10	July 10	10	June 25	10	July 10	10
July 10	10	July 28	7	July 10	10	July 28	7
July 28	10	Aug. 12	6	July 28	6	Aug. 12	1
Aug. 12	10	Sept. 1	9	Aug. 12	10	Sept. 1	5
Sept. 1	10	Sept. 17	[2]	Sept. 1	[2]	Sept. 17	[2]
Sept. 17	10	Oct. 2	10	Sept. 17	10	Oct. 2	10
Oct. 2	10	Oct. 24	10	Oct. 2	10	Oct. 24	6
Oct. 24	9	Nov. 6	9	Oct. 24	9	Nov. 6	5
Nov. 6	9	Nov. 20	6	Nov. 6	9	Nov. 20	9
Nov. 20	10	Dec. 12	9	Nov. 20	10	Dec. 12	9
		1909.				1909.	
Dec. 12	10	Jan. 10	9	Dec. 12	10	Jan. 10	8
1909.				1909.			
Jan. 10	10	Feb. 7	1	Jan. 10	10	Feb. 7	4
Feb. 7	3	Feb. 23	3	Feb. 7	7	Feb. 23	7
Feb. 23	10	Mar. 14	10	Feb. 23	8	Mar. 14	8
Mar. 14	10	Mar. 30	10	Mar. 14	10	Mar. 30	10
Mar. 30	10	Apr. 12	8	Mar. 30	10	Apr. 12	8
Apr. 12	10	Apr. 27	10	Apr. 12	10	Apr. 27	10
Apr. 27	8	May 20	8	Apr. 27	4	May 20	4
May 20	10	June 14	10	May 20	10	June 14	10
June 14	10	June 26	10	June 14	10	June 26	10
June 26	10	July 7	10	June 26	10	July 7	10
July 7	10	July 21	10	July 7	10	July 21	10
July 21	10	Aug. 2	10	July 21	10	Aug. 2	10
Aug. 2	10	[3]	[3]	Aug. 2	10	[3]	[3]

[1] Series sent from Washington, D. C., to Minneapolis, Minn.
[2] Not recorded.
[3] Experiment discontinued.

The lowered percentage of successful infections in July and August of 1907 and 1908 is noticeable and was due to the extreme heat in the greenhouses at the time of inoculation. The uredospore germinates either not at all or not nearly so well at the excessive temperatures of 90° to 100° F. and over, which then existed during parts of each day, as it does in more moderate temperatures, 55° to 75° F.; the germ tubes are injured and the host plants themselves become drawn and weak, reducing the chances for infection very markedly. *Puccinia coronata*, however, is noticeably resistant to heat and *P. rubigo-vera* on wheat is a close second, while *P. graminis* on oats is injured quickly and *P. graminis* on rye is killed by excessive temperatures.

The most important point brought out by these experiments is that for 52 generations there is no apparent diminution of the vitality of the uredo generation due to continuous culture and the absence of the æcidio or teleuto generations. For this length of time, at least, there is no need for a sexual generation. How long successive uredo generations can continue without lowered vitality has not been determined, but these experiments indicate that they may continue for a very long period and that the uredo generation may be all sufficient. It must be noted that the number of successive inoculations in these experiments far exceeds the probable number under ordinary field conditions because they were continued throughout the winter months. Since 8 to 12 days (even up to 20 days and over in unfavorable weather) are necessary for infection and since probably not more than 5 or 6 successive infections follow each other annually in field conditions, the inoculations in the above experiments are equivalent to 7 or 8 years of successive infection in the field.

WINTERING OF THE UREDO GENERATION.

HISTORY OF THE INVESTIGATIONS.

The question whether or not the uredo stage of rusts lives over winter either as mycelium or in the spore form has been a much mooted one ever since De Bary demonstrated the heterœcism of *Puccinia graminis* in 1865. This problem has been investigated by many scientists in different countries and localities.

Germany.—De Bary (12, p. 23) was one of the first of these investigators. He looked for the wintering of the mycelium of *Puccinia graminis* on *Agropyron repens* and *Poa pratensis*, but although heavily covered with rust in the field the same plants in the following spring and summer remained rust free. He concluded that the rust mycelium is annual only, even in perennial grasses.

Kühn (66, p. 401) found the uredo of *Puccinia coronata* in all stages of development on *Holcus lanatus* in the middle of winter and maintained that it developed without hindrance in the spring; on this account he considered a similar wintering in *Puccinia graminis* and *P. rubigo-vera* very possible.

According to Eriksson and Henning (39, p. 38), Blomeyer (20, p. 405) believed that *Puccinia graminis* was able to winter over in the uredo stage at Leipzig on account of the early appearance of *P. graminis* in the spring (latter part of May) at that place.

Klebahn (63, p. 64) says that neither does *Puccinia graminis* appear to winter in the uredo stage nor *P. coronifera avenae* nor *P. simplex*, because oats and barley rarely, if ever, are grown as winter grains in

Germany. He considers the wintering of the uredo of *P. dispersa* (*P. rubigo-vera*) and of *P. glumarum* to be possible.[1]

Denmark. According to Eriksson and Henning (39, p. 38), Rostrup (87, p. 55) considered the wintering of the uredo of *Puccinia graminis* very possible in mild winters in Denmark, especially as it sometimes appears before the æcidium on the barberry.

Sweden.—Eriksson and Henning (39, pp. 40, 41, 131) were unable to find that Puccinia on *Agropyron repens*, *Dactylis glomerata*, and *Agrostis vulgare* winters over in the uredo stage in Stockholm. They were inclined to believe, however, that *Puccinia phlei-pratensis* winters in the uredo.

In a letter from Eriksson to the authors dated December 28, 1907, he states that his conclusions as to the wintering of the uredo of *Puccinia phlei-pratensis* published in Die Getreideroste, 1906, lack sufficient support; that conditions are very probably the same for this rust as for the cereal rusts—i. e., it does not winter in the uredo stage.

The wintering of the uredo of *Puccinia dispersa*, either as spore or mycelium, according to Eriksson and Henning, does not take place in Sweden (39, p. 218), and according to these authors the probability of the uredospore of *P. glumarum*, the yellow rust common in Scandinavia, England, and India, living over winter is very slight, at least in the vicinity of Stockholm.

England.—Plowright (85, p. 234) found uredospores in England on *Agropyron repens* in December, 1881, and again in March; whether *Puccinia graminis* or *P. rubigo-vera* is not absolutely clear. He adds:

> This spring our Norfolk and Suffolk wheats were much affected with rust; some of this may be and probably was due to the *Uredo linearis* kept alive from the previous autumn, but the bulk of it was due to the uredo of *Puccinia straminis* (*P. rubigo-vera*), which is always an earlier uredo than that of *P. graminis*.

The same author (84, p. 35) affirms that the uredo of *Puccinia rubigo-vera* can be found throughout the whole winter in England. Ward (99, p. 132) found viable uredospores of *P. dispersa* on Bromus during every month in the year.

Biffen (17, pp. 241–253) believes that the yellow rust *Puccinia glumarum* also winters in the uredo stage in England. He says:

> The uredospore stage seems to be sufficient to enable the fungus to tide itself over the winter, for it is possible to find pustules of rust on the foliage of self-sown wheat

[1] In an article which has appeared while this paper was in preparation Hecke (Naturwissenschaftliche Zeitschrift für Forst- und Landwirtschaft, vol. 9, pt. 1, Jan., 1911, pp. 44–53) brings forth experimental evidence to show that the uredo mycelium of yellow rust, *Puccinia glumarum*, winters over in the leaves of the winter grains at Vienna, Austria. He inoculated winter wheats in pots October 28 and November 21, 1909, left them in the greenhouse for three days, and brought them into the open, where they remained all winter. Pustules of yellow rust appeared March 28, 1911, on the inoculated leaves, while control leaves remained rust free. In this instance the incubation period of this rust must have been four and five months, during which time the mycelium remained practically dormant.

or sometimes on the ordinary autumn-sown crops even in the depths of winter. The twisted leaves lying on the soil form a series of sheltered, moist chambers, on the inner surface of which the rust pustules are occasionally present in great numbers. These may develop with rapidity in the early spring, and at times as early as March the whole of the plant's foliage may be yellow with rust. The winter's cold does not appear to injure these spores, for they germinate readily when brought into the laboratory, and there can be little doubt that they serve to start the epidemic in the spring, when conditions become favorable for infection. Under these circumstances it is not necessary to assume that the first appearance of any fungus in any season is dependent upon its being actually present in the embryo of the grain, spreading therefrom as the plant develops and ultimately producing its spores when the external conditions are favorable.

Australia.—McAlpine (74, p. 27) believed it probable that the red-rust spores survive the winter in Australia and reproduce the fungus again in the spring or summer.

Cobb (36, p. 186) says:

> During the past two years it has been proved that the wheat rusts, that is, *Puccinia graminis* and *P. rubigo-vera*, exist in the uredo stage all the year around in Australia.

McAlpine (76, p. 20), from further observations on the wintering of rusts in Australia, says:

> When the winter is mild and green vegetation flourishes, the mycelium of the rust fungus may continue to grow and may even produce spores; whereas, if the winter is severe and the mycelium does not remain in the perennial part of the plant, then the continuance of the fungus is likely to be by teleutospores, which can last through the winter on dead stems or other decaying vegetable matter. The so-called wintering of the uredo depends so much on the climate that in a mild climate the fungus may perpetuate itself exclusively by uredospores; whereas under severe conditions it has to resort to teleutospores.

He further observes that in Australia it is the heat and drought of summer which the rust must withstand, not the cold of winter, and hence *Puccinia graminis* produces only comparatively few teleutospores and lives over in the uredo stage in that country. During the winter it is found in abundance on volunteer grains.

The same author cites numerous instances of the germination of the uredospore during winter. He says (76, p. 22):

> The uredo may become inured to unfavorable conditions, such as drought or cold, and carry on the life of the species independent of the teleutospore.

Such adaptation is seen in this country in *Puccinia vexans* Farl., which, in addition to the ordinary uredo, has a specialized form, a thick-walled, strongly papillate amphispore which germinates only after a period of rest (31, pp. 22–25).

United States.—Bolley in 1889 (21, pp. 13, 14) proved by a series of observations that *Puccinia rubigo-vera* on wheat near Lafayette, Ind., can pass the winter as "healthy fungal mycelium within the tissues of the leaves," producing rust spores in abundance at the first appearance of warm weather in March. "The very early appearance

and prevalence of red rust, *Puccinia rubigo-vera*, is attributed in part to the ability of that species to winter its mycelium" (21, p. 14). Apparently the same instance is cited by him in a later publication (22, p. 107).

The same author in 1891 (23, p. 260) says:

> The red rust (uredo of *P. rubigo-vera* and *P. coronata*) is developed to a greater or less extent during all months of the year in States south of Tennessee. * * * In the States north of this line there seem to be isolated cases in which the mycelium may persist through winter, dependent, apparently, chiefly upon the point whether the attacked portion of the host persists or not.

Hitchcock and Carleton (57, p. 11; 29, p. 453) found in Kansas throughout the winter months (January 23–25, February 25, and March 1) viable uredospores of *Puccinia rubigo-vera* on wheat. They state:

> It would seem that the uredospores were not formed during the winter, but had retained their vitality since the preceding fall.[1]

Again, Bolley (24, p. 894) says that fresh uredospores of *Puccinia rubigo-vera* can be found in the United States throughout the winter in States south of Ohio, and although new spores are not formed in States as far north as Indiana and Kansas during the coldest periods, those already formed retain their viability.

Carleton (30, p. 21), in speaking of the uredo of *Puccinia rubigo-vera* on wheat, says that the conclusions of Bolley, Hitchcock, and Carleton as to the wintering of the uredo have been confirmed and reconfirmed by him both in Kansas and in Maryland.

> In the Southern States the leaf rusts of both wheat and rye not only live but grow all winter. * * * In latitudes below 40° in this country, leaf rust of wheat is able to pass a perpetual existence in the uredo stage on wheat alone, without intervention of any other stage.

Again he maintains (30, p. 44) that *Puccinia rubigo-vera secalis* lives over winter in a similar manner, and it is his opinion that this rust "readily passes the winter as a uredo in all parts of the United States." He found the uredo in great abundance in a patch of volunteer rye at Lincoln, Nebr., in November, 1897, and afterwards in midwinter in the same place. April 15, 1898—

> it was still present in considerable quantity, but was confined entirely to the leaves of the previous autumn's growth and had without question lived through the winter, though the leaves were still somewhat green.

Some of the uredospores germinated in water-drop cultures. Two days later the uredo was found in considerable quantity several miles from this locality.

> In neither case was there any production of new spores, and yet the spring was so far advanced that there could be no question about the continual growth of the rust.

[1] The minimum temperatures (F.) at this time were: For December, −9°; January, −1°; February, −6°.

He did not demonstrate the wintering of the uredo of *Puccinia coronata* on oats, *P. graminis tritici*, or *P. graminis avenae*, although it is his opinion that *P. coronata* passes the winter in the uredo stage in the warm latitudes of the United States (30, pp. 49, 57, 64).

In 1902–3, Christman (32, pp. 103, 104) showed that in the locality of Madison, Wis., the uredospores of *Puccinia poarum* would winter and germinate as late as March 13; of *P. rubigo-vera secalis* and *P. rubigo-vera tritici*, March 20. Numerous other collections and germinations were made throughout the winter from plants in exposed places, and the author concludes that—

> in the latitude of Madison and with a period of three months during which the temperature scarcely rises above the freezing point, viable uredospores may be obtained at practically any time during the winter.

In investigations during the winter of 1904–5, Bolley (28, p. 642) obtained a collection of viable uredospores of *Puccinia rubigo-vera* in December and January in Kansas, Oklahoma, Missouri, Illinois, Wisconsin, Minnesota, and North Dakota. Viable uredospores of *P. graminis* were collected late in October at St. Louis, and December 25 at Dallas, Tex. In January—

> quantities of them were being procured upon winter wheat at Riverside, Ill. Later some were procured in quack-grass at Lake City, Minn., and a quantity of viable spores were taken from the leaves of quack-grass and wild barley frozen in the ice at Fargo in March, 1905.

RECENT EXPERIMENTS ON THE WINTERING OF THE UREDOSPORE.

During the winter of 1906–7, the authors undertook to establish the extent of viability of the uredospore of various rusts in the vicinity of St. Paul, Minn. All material was collected on or near the Minnesota Agricultural Experiment Station farm.

In the early fall suitable plants of *Hordeum jubatum*, *Agropyron repens*, *A. tenerum*, winter wheat, and fall-sown barley were selected. These were left undisturbed in the open field at the University farm. They had become thoroughly infected by either *Puccinia graminis*, *P. rubigo-vera*, or both. During the fall and winter, collections of uredospores were made from all hosts, selected every month and at times at intervals of two weeks.

Portions of the various hosts were also collected November 20 and 23 (1906); these were kept outside, were buried in snow December 10, and left in this condition until March 20, 1907. Every month specimens from this supply were tested in the same manner as the material brought from the field.

All tests were made in distilled water in watch crystals placed under a bell jar and kept at ordinary living-room temperature or a little above. In many instances the percentage of spores that germinated was determined by actual count, but generally rough estimates only were made.

Dates of collection and germination and summary of results are given in Tables IV and V.

TABLE IV.—*Summary of experiments on the wintering of the uredospore at St. Paul, Minn.*

Date of collection and germination test.	Species.	Host plant.	Time of incubation.	Germination.
			Hours.	*Per cent.*
November 20, 1906	Puccinia graminis	Hordeum jubatum	22	95
December 14, 1906	do	do	40	26
December 27, 1906	do	do	24	50
January 25, 1907	do	do	22	30
February 15, 1907	do	do	24	75
March 16, 1907	do	do	18	50
April 15, 1907	do	do	26	35
November 20, 1906	do	Agropyron repens	22	50
December 14, 1906	do	do	40	3
December 27, 1906	do	do	24	32
January 25, 1907	do	do	22	5
February 15, 1907	do	do	24	25
March 16, 1907	do	do	18	50
April 15, 1907	do	do	26	5
November 20, 1906	do	A. tenerum	48	5
December 14, 1906	do	do	40	25
December 27, 1906	do	do	24	95
January 25, 1907				
February 15, 1907	P. graminis	A. tenerum	24	10
March 16, 1907	do	do	18	25
April 15, 1907	do	do	26	40
November 29, 1906	P. rubigo-vera	A. repens	22	50
December 14, 1906	do	do	40	10
December 27, 1906	do	do	24	50
January 25, 1907	do	do	22	50
February 15, 1907	do	do	24	0
March 16, 1907				
November 20, 1906	P. rubigo-vera	Winter wheat	40	15
December 14, 1906	do	do	40	20
December 27, 1906	do	do	24	12
January 25, 1907	do	do	22	25
February 15, 1907				
April 16, 1907				
November 20, 1906	P. simplex	Barley		
December 14, 1906	do	do	40	30
December 27, 1906	do	do	24	40
January 25, 1907				
February 15, 1907				
March 16, 1907				

TABLE V.—*Summary of germination results from uredo material kept buried in snow until germination tests were made.*

Date of germination test.	Species.	Host plant.	Time of incubation.	Germination.
			Hours.	*Per cent.*
December 10, 1906	Puccinia graminis	Hordeum jubatum	20	50
January 8, 1907	do	do	24	5
February 9, 1907	do	do	24	5
March 20, 1907	do	do	20	15
December 10, 1906	do	Agropyron repens	20	25
January 8, 1907	do	do	24	90
February 9, 1907	do	do	24	25
March 20, 1907	do	do	20	75
December 10, 1906	do	A. tenerum	20	40
December 10, 1906	P. rubigo-vera	A. repens	20	60
January 8, 1907	do	do	24	30
February 9, 1907	do	do	24	10
March 20, 1907	do	do	20	50
December 10, 1906	do	Winter wheat	20	25
January 8, 1907	do	do	24	3
February 9, 1907	do	do	24	5
March 20, 1907	do	do	20	10
December 10, 1906	P. simplex	Barley	20	15
January 8, 1907	do	do	20	10
February 9, 1907	do	do	24	50
March 20, 1907	do	do	20	10

The wide variation in percentage of germination in collections made at different times in these experiments is principally due to the fact that spores at the same stage of development and equally well protected can not be obtained twice in succession. It was noticeable that those spores which were just mature and remained well protected under the epidermis of the host were the most viable. In a large number of cases such spores seemed to be as healthy in the spring as they were in the fall. Those spores which broke through the epidermis, dropped off from the old mycelium, and rested loosely in the leaf sheath, seemed to lose their power of germination during the winter and would not germinate in the spring.

The winter of 1906–7 in Minnesota was not abnormal, and much of the rust material collected was dug from under the snow and ice. A thaw during a part of January incased much of the material in frozen snow. About February 15 there was another thaw, and the *Agropyron repens* material in particular became incased in ice, which disappeared during the latter part of March.

The tables show that a large per cent of the uredospores of *Puccinia graminis* on *Hordeum jubatum*, on *Agropyron repens*, and *A. tenerum*, collected from plants in the field, germinated throughout the winter, such germinations having been made November 20, December 14 and 27, January 25, February 15, March 16, and April 15. After April 15 such spores were extremely hard to find in the locality under consideration, as most of them had germinated in the warm, humid days of early spring. Uredospores of the same rusts on *Hordeum jubatum* and *Agropyron repens*, collected November 20 and 23, kept outside until December 10 and then buried in snow, germinated on December 10, January 8, February 9, and March 20. After that date the snow disappeared and the material could be kept no longer. The uredospores on *Agropyron tenerum* were tested only on December 10, on account of the scarcity of the material.

Similar experiments with *Puccinia rubigo-vera* gave successful germinations from material on *Agropyron repens* from the field November 29, December 14 and 27, and January 25, while the small amount collected on February 15 did not germinate; from material on *Triticum vulgare* (winter wheat) successful germinations were made November 20, December 14 and 27, and January 25, while after that date no material could be obtained; *Puccinia simplex* on barley collected in the field germinated November 20, December 14, and December 27. After that time no more could be found.

Material of all three of these leaf rusts collected on their respective hosts November 20 and 23, kept outside until December 10 and then buried in snow, germinated December 10, January 8, February 9, and March 20. After that date no trials were made.

The uredospores of *Puccinia graminis* on *Hordeum jubatum*, *Agropyron repens*, and *A. tenerum* obtained from the natural field habitat have thus been demonstrated to retain their viability until April 15, and material from the two former kept buried in the snow until March 20 has also been shown to remain viable. *Puccinia rubigo-vera* on *Agropyron repens* and *Triticum vulgare* from the field have been demonstrated to germinate as late as February 15, and *Puccinia simplex* on *Hordeum vulgare* as late as December 27. After these dates no material could be obtained. A large per cent of the uredospores collected in the fall and kept buried in snow since December 10 germinated as late as March 20, 1907. Bolley has shown that spores of *Puccinia rubigo-vera* collected in Minnesota April 9 and in North Dakota April 13, 1905, were viable (28, p. 649). Together with Bolley's and Christman's investigations cited above, these experiments demonstrate conclusively that it is possible for the uredospores of various stem and leaf rusts to retain their viability throughout the winter in Minnesota, North Dakota, and Wisconsin.

How commonly the wintering of the uredospore in these northern States takes place is yet to be determined. Where snow remains throughout the winter, preventing alternate freezing and thawing of material thus covered, the wintering of the uredospore is, perhaps, facilitated. Indeed, it is very probable that the uredospore survives the winter more easily in the north, where snow is continuous during the winter, than in localities where snow covers the ground only at intermittent periods. Then, there is probably as good a chance, if not better, for the uredospore to winter in northern Minnesota or southern Canada, as in southern Minnesota or Iowa. This view is also held by Bolley and Pritchard (28, p. 643).

From Kansas south, it has been proved by Hitchcock and Carleton (57, p. 11) that *Puccinia rubigo-vera* winters very easily in the uredo stage, and undoubtedly this also holds true for *P. graminis*. In the springs of 1908 and 1909, the authors personally observed wheat fields in Texas and Oklahoma. During the latter part of April, 1908, both *Puccinia graminis* and *P. rubigo-vera* were extremely abundant on wheats at San Antonio, Tex. Farther north, at Amarillo, Tex., *P. rubigo-vera* was well scattered April 30, though not plentiful. At Stillwater, Okla., May 7, this rust was abundant. Wheats at San Antonio, in 1909, were heavily rusted April 4, with both *P. graminis* and *P. rubigo-vera*, and the superintendent of the San Antonio Experiment Farm said that a rust was abundant in the grain plats in February.

There is, then, an abundance of rust spores in southern wheat fields in the early spring, and, according to investigations cited in this paper, there are also a large number of uredospores of *Puccinia*

graminis and *P. rubigo-vera* which have survived the winter in the north and are ready to infect the growing grain.

The great problem for rusts in many places of the South, however, is not how to live over the winter, but how to pass through the extremely hot months of July, August, and September. This is especially true of the cereal rusts in portions of eastern and southern Texas, as volunteer grain is scarce at that time; but in northwest Texas the authors noticed vigorous rust pustules of both *Puccinia graminis* and *P. rubigo-vera* on volunteer wheat during September, 1907, so that in the higher altitudes in the Southwest the rust does exist in the uredo form on volunteer grain in late summer and early fall. The early-sown fall wheat can thus become infected with spores from this source, as described later in this paper.

DISSEMINATION OF THE UREDOSPORE.

METHODS OF DISSEMINATION.

Rusts in the uredo stage have been shown to be present in parts of both the North and South at almost all times of the year, and in order to explain their constant menace to the crops of the country it remains only to determine their means of dissemination. Rust spores are extremely numerous, hundreds occurring in a single pustule. They are very light, much more so than dust particles, which have been known to be carried in the air for hundreds of miles and distributed over large territories in a few days. An example of the carrying power of the air is cited by Klebahn (63, pp. 66–68) who relates that dust clouds arising in northern Africa, March 9, 1901, were driven over a large part of the continent of Europe in the next two days. Corresponding dust showers were noticed March 9 and 10 in Tunis, West Tripoli, and Algiers; early March 10 in southern Sicily; night of March 10–11 in the East Alps; early March 11 in Maingebiet; at 4.30 in the afternoon in Hamburg; and a little after midnight in the Danish Islands (Stege auf Moen). The dust was composed of clay, fine quartz particles, and other minerals, supposedly derived from the African deserts.

Undoubtedly, rust spores, which are much lighter than these dust particles, can be carried more easily by the wind and air currents over as great, if not greater, distances. Rising into the air, these spores may reach the upper atmosphere and be carried hundreds of miles a day in whichever direction the air currents are moving. In this way innumerable rust spores may be carried from regions where they are plentiful, either by reason of the presence of the æcidial hosts, or overwintering uredos, to regions where grain is in a receptive condition. This interchange of spores between localities may take

place mainly from south to north in early spring and summer and from north to south in late summer and fall. Together with the wintering uredos in the North, such wind-carried spores from the South undoubtedly can cause early infection of the grains, and together with the spores on volunteer grains in the South the spores from the Northern States wafted south may serve to infect the winter grains as they come up in October and November.

That large quantities of rust spores are present in the air at various times has been proved by many investigators. Klebahn (63, pp. 69, 70) constructed cotton plates, leaving them in the open in trees in different places in Germany in the spring and summer at different periods. These cotton plates were then taken down and washed out carefully, and the water examined. Several thousand uredospores of *Puccinia graminis* and other rusts were found in each cotton mass, as well as innumerable spores of other fungi. Æcidiospores and teleutospores were found very sparingly. Klebahn concludes that numberless spores are contained in the air and large numbers fall on a proportionally small space. He believes that since grains are almost universally cultivated, and are scarcely ever rust free, tremendous numbers of rust spores are carried into the air in every grain-growing country, and, as a consequence, there is a universal distribution of them.

Experiments on this point have also been performed by the authors. On May 22, 1907, plates containing water were exposed for four hours at a time on top of one of the university buildings at Minneapolis, Minn., and also in an adjoining garden. On centrifuging this water and examining the sediment several uredospores were found, of both *graminis* and *rubigo-vera* types. Several teleutospores of *Puccinia graminis* were also found. E. C. Stakman performed similar experiments at St. Anthony Park, Minn., in April and May, 1910. Plates with water were exposed in the field, outside the laboratory window, and at the top of a water-tank tower at a height of 100 feet or more. The direction of the wind was southeast. April 11, in a plate exposed outside the laboratory window for four hours, several uredos of a *graminis* form were found. April 11 and 12, from a plate exposed for 48 hours in the field, several uredos were found; and on the same dates in a plate exposed for 48 hours on top of the water tower over 100 feet high, several uredospores of the *graminis* form were secured. On May 11, Stakman made a similar test and succeeded in germinating a uredospore of *Puccinia graminis* collected from the air at this time. These experiments of 1907 and 1910 were performed before uredospores began to appear in the field in new growth in that locality, and the spores must have come either from uredos wintering over in the North or from uredos borne from the wheat fields in the

South where fresh uredos of both *Puccinia graminis* and *P. rubigo-vera* forms are plentiful at this time of the year. This furnishes substantial evidence that Klebahn's suppositions are correct, and rust spores may be considered fairly universal in distribution.

VIABILITY OF THE UREDOSPORE.

That spores can resist desiccation in air and maintain their viability when transported long distances has been proved by Bolley (24, p. 892). In July, 1898, he demonstrated that uredospores of *Puccinia rubigo-vera*, exposed for 12 days on a dry watch glass placed in the sunlight, would germinate 80 to 100 per cent, and on August 4, spores placed in a similar place for 21 days would germinate from 5 to 10 per cent. July 25 and August 4, 1898, respectively, the same investigator proved that the uredo of *P. graminis* would give "good" germination after being exposed for 12 days on a watch glass in direct sunlight, and gave 8 to 15 per cent germination after 21 days on a watch glass in a similar position.

Ward (102, p. 13) found that uredospores of *Puccinia dispersa* germinated after being kept dry for 61 days; and Miss Gibson, working in his laboratory, kept æcidiospores of Phragmidium for 54 days and uredospores of chrysanthemum rust for 94 days, when they still germinated. Carleton (31, pp. 21, 22), February 3, 1898, germinated uredospores of *P. cryptandri* collected in Oklahoma, October 8, 1897, and kept as herbarium specimens, and got successful infection on *Sporobolus airoides* from inoculations made February 6 from the same material. This is an extreme case of the viability of the uredospore when kept in a dry condition.

The authors have numerous times shipped uredo material of the cereal rusts through the mails from Minnesota to Washington, D. C., and vice versa, and from Texas to Washington, D. C., and have experienced no difficulty in producing successful infection on growing plants, even after these spores had been lying in the laboratory for several days after their arrival. The uredospore is thus seen to be sufficiently resistant to be transported long distances in a dry condition by either the wind or other agencies.

FIRST APPEARANCE OF RUSTS IN THE SPRING.

From the facts cited concerning the viability of the uredospore and its almost universal distribution, the first spring infection of grains in northern latitudes and the infection of grains far removed from the æcidial hosts of the rusts may be explained. Careful observations on the first appearance of rusts in the spring were made at Minnesota in 1907, 1908, and 1909. In 1907, *Puccinia rubigo-vera* on winter wheat was common up to the middle of April, when

the old leaves died and the rust disappeared, not being noticed again until June 21. In 1908 this rust was first found in the field June 18, and in 1909, June 9. *P. graminis* was first found on winter wheat July 26, 1907, July 3, 1908, and July 5, 1909, while æcidia on barberries were producing spores in 1907 about June 15, in 1908 about June 1, and in 1909 between June 14 and 26. Generally speaking, *P. rubigo-vera tritici* and æcidia on barberries appear at St. Paul, Minn., about the middle of June, and *P. graminis tritici* the first half of July—that is, from two to three weeks after the other two.

Puccinia rubigo-vera is believed not to have any æcidial stage in this country. If this is so and the impossibility of direct infection from the teleutospore is granted, the appearance of this rust in spring must be accounted for by infection from wintering uredo, either as mycelium or spore, or by infection from wind-borne spores from fields farther south. Both methods are possible, and both undoubtedly may be employed. That viable uredospores of this rust have not been found between April 15 and the first part of June in the locality under consideration might furnish some argument that infection from wintering uredos is not possible. Considerable light is thrown upon this question by a study of the difference in length of incubation period of rusts under varying conditions. Under the cool temperatures of early spring the incubation period—that is, the time from inoculation until pustules appear—is lengthened from 7 to 10 days in warm weather to between 3 and 4 weeks and possibly more in cool weather. This lengthened incubation period under cool temperatures has been noticed many times by various investigators.

In 1910, experiments on this point were performed in warm and cool greenhouses at Washington, D. C. A large number of oat plants were inoculated with the uredo of *Puccinia graminis* February 3, 1910. Half of them were placed in a house where the temperatures ranged between 42° and 67° F., reaching 70° F. for an hour or two February 8 and 14, and the other half were placed in a greenhouse where the temperatures ranged between 62° and 90° F. On the plants kept in the cool house pustules began to appear after a period of 18 days, while on the plants kept in the warm house pustules were abundant after 8 days. *Puccinia graminis* on wheat under similar conditions began to show pustules after 16 days on plants kept in the cool house, while pustules were abundant after 6 days on plants kept in the warm house. Could the temperatures in the cool house have been kept consistently lower than those indicated, undoubtedly the incubation period would have been considerably lengthened. Christman (32, p. 106) made similar observations in 1903 at Madison, Wis. He noticed an early outbreak of uredospores of *Puccinia rubigo-vera* on winter wheat and rye between March 20 and April 3, 1903. This

disappeared, and from April 8, a period of about four weeks, it was impossible to find a single spore. On May 6 new leaves began to show a diseased appearance. On May 13 open pustules were found in abundance. He states further that he has found by experiments that in the cooler weather of spring the incubation period following inoculation with uredospores is lengthened to between three and four weeks, and this explains the existence of a period with no rust after the first attack.

The winter leaves die in the early spring and with them the winter mycelium, but not until it has produced uredospores which inoculate the new leaves. Then follows a period of incubation which may be lengthened more or less according to the temperature and other conditions in the spring.

This, then, is one way to account for the spring appearance of *Puccinia rubigo-vera* in the middle Northwest. The other way is the infection of the grains from spores carried in the air from the South. It has been shown in this paper that *P. rubigo-vera* winters in the vegetative uredo stage in Kansas and Nebraska, producing spores on the winter grains in March and April. This is true, also, of a large part of the Atlantic Coast States, particularly Maryland and Virginia. These spores may be carried by the winds farther north during the months of April and May, becoming generally distributed. Inoculation may then be cumulative—i. e., spores may fall on fields from time to time during several weeks in April and May without any apparent effect. Then, when moisture and temperature conditions become just right, a general, though sparing, outbreak may take place over large territories within a few days. After this first outbreak spores will be present in abundance and the attack may spread rapidly.

Puccinia graminis in the Middle Northwest makes its first appearance from two to three weeks after the appearance of æcidia on barberries. From this it may be argued that the first infection always comes from the æcidiospore. Barberries are grown as hedges and ornamental shrubs here and there in the Middle Northwest, and certainly are the cause of more or less local æcidiospore infection, but the appearance of *P. graminis* over large territories within a few days is to be accounted for in other ways. The wintering of the uredo in the North and also wind-blown spores from southern fields in the progressive northward march of this rust are, perhaps, the most important agencies in its first appearance, just as in the case of *P. rubigo-vera*. Another possibility is the transfer of the uredo of *P. graminis* from the wild grasses, especially *Hordeum jubatum*, *Agropyron repens*, and *A. tenerum*. Viable uredos have been found in these grasses as late as April 15, and undoubtedly occur even later in the season. That the *graminis* form on these grasses may affect wheat has been demonstrated; but the new crop of uredospores on

these grasses in the Dakotas and Minnesota generally appears later than the uredo in the cereals, so that the first infection, if it comes from them, must come from wintering uredos.[1]

Careful studies of the wintering of *Puccinia coronata* and *P. graminis* on oats have not been made and a discussion of them is omitted. Undoubtedly the first appearance of these rusts in the spring will also be found to result from wintering uredos and wind-borne spores.

EPIDEMICS.

GENERAL DISCUSSION.

At irregular intervals of several years wheat-rust epidemics, more or less general, occur throughout the country. That these depend to a great extent on climatological conditions is quite generally believed. Periods of excessive rainfall, followed by warm, muggy days, are supposed to be favorable to their development. Why this should be so is not generally understood, and numerous instances where epidemics have not occurred, even after such climatological conditions, might be cited. On the other hand, in some parts of the country, south-central Texas for instance, rust is abundant almost every year in spite of frequent droughts during the maturing period of the grain.

CONDITIONS FAVORABLE FOR AN EPIDEMIC.

At least three conditions must be fulfilled before an epidemic can occur: (1) A sufficient number of rust spores must be present on the growing grain to give the fungus a start; (2) the humidity and temperature conditions must be favorable for the germination of these spores and consequent infection; (3) the grain must be in a receptive condition.

The first condition, very probably, is satisfied almost every year in the main grain-growing regions by the presence of overwintering uredos, wind-blown uredospores, or æcidiospores. However, if such spores are unusually abundant, as they may be after a favorable

[1] A full discussion and consideration of Eriksson's mycoplasm theory published in Compt. Rend., 1897, pp. 475–477, and further treated in Eriksson's later publications, is omitted for lack of space. In this theory Eriksson holds that the rust fungus "lives for a long time a latent symbiotic life as a mycoplasma in the cells of the embryo and of the resulting plant, and that only a short time before the eruption of the pustules, when outer conditions are favorable, it develops into a visible state, assuming the form of a mycelium." External infection is given only secondary importance. This theory has been severely criticized by H. Marshall Ward in "History of Uredo dispersa Erikss., and the 'Mycoplasm hypothesis.'" Philosophic Transactions of the Royal Society, series B, vol. 196, pp. 29–46, and in "Recent Researches on the Parasitism of Fungi," Annals of Botany, vol. 19, 1905, pp. 1–45, and Klebahn (63, pp. 72–76). Eriksson defends his position in Arkiv für Botanik, vol. 3, 1905, pp. 1–54, and in later articles. The subject is still a live one and readers are referred to the various authors cited for full discussions of it. The authors of this bulletin have found no evidence which can be said to substantiate the mycoplasm theory. On the other hand, the wintering over of the rusts, as shown above, can be reasonably explained without the assistance of Eriksson's theory.

winter and spring, the first infection may be heavy and widespread and the chances for an epidemic may be increased in proportion. Thus, the presence and unusual rustiness of barberries in any one district and consequent abundance of æcidiospores in that district are favorable for a local epidemic, and an abundance of uredospores produced on winter grains in mild climates, or wintering in colder climates and then distributed by the wind, may have the same effect over wider areas. That such wintering uredos and wind-blown spores are usually present in sufficient quantities to give the rust a good start is fairly well established. The multiplication and dissemination of these spores may extend over a period of several weeks and may even be facilitated by periods of dry, windy weather under temperature and moisture conditions in which germination will not take place.

Whether or not these spores cause infection after falling on the grain depends upon various conditions. Sudden showers at this time undoubtedly wash off many of the spores before germination occurs, while fairly humid conditions and moderate temperatures are not only favorable but almost absolutely necessary for infection. Cool nights with an abundance of dew and humid, misty days in which the grain remains moist from 12 to 24 hours at a time are exceedingly favorable and are far better than periods of excessive rainfall, due to sudden showers, with periods of hot sunshine between. Contrary to the general belief, moderately cool and even subnormal temperatures are more favorable for spore germination and infection of the grain than higher temperatures. Thus, in the excessive temperatures which often occur in the Middle Northwest in July and August, it is exceedingly difficult to produce rust infection by many of the rusts even though moisture and other conditions are favorable.

Marshall Ward (98, p. 233) has shown that in the case of the brown rust of bromes, *Puccinia dispersa* Erikss., germination of the uredospore will not take place at temperatures much above 26° to 27.5° C. (78.8° to 81.5° F.) or below 10° to 12° C. (50° to 53.6° F.), will not germinate at all at 30° C. (86° F.), and will produce maximum germination at about 20° C. (68° F.). The different species and varieties or biologic forms of rusts vary somewhat in this respect, but moderately cool temperatures are more favorable for germination (and consequent infection) of the uredospore of most of them than excessively high temperatures. Even after infection has taken place excessive temperatures may inhibit to some extent the development of the rust, while moderate temperatures will aid its development.

The presence and germination of rusts being accounted for, it remains to be seen when the grains are in the most receptive condition. In 1908 and 1909 the authors investigated this point for

Puccinia graminis both in Texas and Minnesota. Hundreds of wheat plants in field conditions were inoculated with spores of *P. graminis* by pouring over the head and culm water filled with fresh spores. Plants at all stages of development, from the time when the head was still in the boot to the time when the grains were half filled, were used for the inoculations. It was found that plants inoculated from the time when the heads emerge from the boot until they are in full bloom rusted far more than plants inoculated either before or after this stage of development. Just why the wheat should be very susceptible to a rust attack at this time requires further study. There may be a particular physiological weakness due to the rapid growth and abundant elaboration of starch at this period and the susceptibility of the grain may be increased on that account. Whatever may be the cause, the critical period for wheat with regard to attacks of *P. graminis* is during the heading time, a period of about 10 days for any one locality. If for any reason this period is delayed or lengthened, the number of uredospores falling on each plant is very considerably increased, infections have a longer time in which to develop, and the danger of an epidemic is imminent.

CLIMATOLOGICAL CONDITIONS IN RELATION TO RUSTS IN 1903, 1904, AND 1905.

To determine how closely the conditions favorable for rust epidemics have been approximated in years of severe rust, a study has been made of the climatological conditions over the important wheat States in the Mississippi Valley from the Gulf to Canada for the years 1903, 1904, and 1905. Rusts were fairly abundant in 1903, though not strikingly so. In 1904 an epidemic occurred which was particularly severe over North and South Dakota, Minnesota, and parts of Iowa, while in 1905 the rust, though not epidemical, was present in great abundance, causing considerable damage in certain localities, particularly in North Dakota and South Dakota.

Wheat heads out in April in southern Texas; in May in northern Texas and Oklahoma, Kansas, and Missouri; in June in Nebraska and Iowa; and in July in South Dakota, Minnesota, and parts of Wisconsin. These three months, then, include the critical period for the several States, that is, the period when rust infection develops and an epidemic, if it occurs, gets its initial impulse. The critical period at any one place would normally not extend over 10 days or two weeks.

PRECIPITATION.

Table VI summarizes the precipitation records for several periods in 1903, 1904, and 1905 in the important wheat States mentioned above.

TABLE VI.—*Precipitation records, showing average monthly departure in inches from normal in several States in 1903, 1904, and 1905.*

1903.

Month.	Texas.	Oklahoma.	Kansas.	Missouri.	Nebraska.	Iowa.	South Dakota.	North Dakota.	Minnesota.	Wisconsin.	Average.
October	+0.47										
November	+4.30	+3.59	+0.64	+1.36							
December	− .20	+ .19	+ .22	+ .71	+0.70	+0.85					
January	+1.4	−5.7	−4.2	− .69	− .38	− .74	−0.18	+0.23	−0.22	−0.88	
February	+4.05	+2.57	+ .98	+ .41	+ .72	+ .09	+ .18	− .10	− .15	− .65	
March	+ .53	+ .50	+ .01	.00	− .43	− .53	− .20	− .39	+4.4	+ .56	
April	−1.90	−1.54	+ .23	− .10	− .69	− .03	− .70	− .56	+ .36	+ .35	
May		+1.57	+4.46	+2.10	+3.62	+4.52	+1.10	+ .70	+2.13	+1.43	
June					−1.65	−1.52	−1.04	−2.51	−2.38	−2.46	
July							+1.55	− .50	+1.50	+2.20	
Departure from normal:											
Accumulative	−8.65	+1.18	+2.34	+3.79	+ .89	+2.64	− .61	−3.13	+5.64	+ .55	+0.46
Average monthly	−1.23	+ .16	+ .33	+ .54	+ .12	+ .37	− .08	− .44	+ .80	+ .07	+ .06
Of 3 crop months—											
Accumulative	+2.68	+ .53	+4.70	+2	+1.28	+2.97	+1.61	−2.31	+6.01	+1.17	+2.06
Average monthly	+ .89	+ .17	+1.23	+ .66	+ .42	+ .99	+ .53	− .77	+2	+ .35	+ .68
Of month containing critical period	−1.90	+1.57	+4.46	+2.10	−1.65	−1.52	+1.55	− .50	+1.50	+2.20	+ .78

1904.

October	+0.11										
November	−2.48	−1.99	−0.04	−1.14							
December	− .92	−1.18	− .61	− .77	−0.52	−0.88					
January	−1.41	+ .12	− .30	+ .86	− .12	+ .21	−0.17	−0.14	−0.31	−0.71	
February	− .08	−1.07	−1.03	−1.34	− .53	− .63	+ .04	+ .21	+ .10	− .02	
March	−1.17	−1.08	− .13	+ .89	− .57	+ .35	− .99	+ .38	+ .05	+ .41	
April	+ .20	− .47	+ .91	+1.97	− .51	+ .74	− .75	− .17	− .73	− .80	
May		+ .23	+1.86	+ .22	+ .02	− .35	− .23	− .57	− .75	+ .17	
June					− .74	−1.05	+ .43	+1.74	+ .05	− .70	
July							− .16	− .38	+ .44	− .72	
Departure from normal:											
Accumulative	−5.55	−5.44	+ .66	+ .69	−2.99	−1.61	−1.83	+1.09	−1.25	−2.37	−1.86
Average monthly	− .79	− .77	+ .09	+ .09	− .42	− .23	− .26	+ .15	− .17	− .39	− .26
Of 3 crop months—											
Accumulative	−1.05	−1.32	+2.63	+3.08	−1.25	− .66	+ .04	+ .79	− .26	−1.25	+ .07
Average monthly	− .35	− .44	+ .87	+1.02	− .41	− .22	+ .01	+ .26	− .08	− .41	+ .02
Of month containing critical period	+ .20	+ .23	+1.86	+ .22	− .74	−1.05	− .16	− .38	+ .44	− .72	− .01

1905.

October	+0.44										
November	−1.46	−1.88	−1.01	−2.09							
December	− .39	−1.06	− .33	− .67	−0.39	+0.15					
January	− .67	+ .64	+ .07	− .29	+ .59	+ .06	+0.16	−0.25	−0.09	−0.04	
February	+ .81	+ .01	− .12	− .54	+ .06	+ .53	− .12	− .21	− .18	− .04	
March	+2.28	+1.93	+1.14	− .33	+ .19	+ .20	− .15	− .15	− .29	− .18	
April	+3.44	+1.58	− .33	− .58	+ .93	+ .14	−1.33	−1.39	− .93	−1.11	
May		+1.38	+ .45	+ .03	+2.04	+1.82	+3.37	+1.18	+2.13	+1.64	
June					+1.24	+1	+2.40	+ .68	+2.39	+3.20	
July							+1.28	+1.44	+ .59	− .31	
Departure from normal:											
Accumulative	+4.45	+2.60	− .13	−4.47	+4.66	+3.90	+5.61	+1.30	+3.52	+3.16	+2.46
Average monthly	+ .63	+ .37	− .01	− .63	+ .66	+ .55	+ .80	+ .18	+ .50	+ .45	+ .35
Of 3 crop months—											
Accumulative	+6.53	+4.89	+1.26	− .88	+4.21	+2.96	+7.05	+3.30	+5.11	+4.53	+3.89
Average monthly	+2.17	+1.63	+ .42	− .29	+1.40	+ .98	+2.35	+1.10	+1.70	+1.51	+1.29
Of month containing critical period	+3.44	+1.38	+ .45	+ .03	+1.24	+1	+1.28	+1.44	+ .59	− .31	+1.05

The precipitation records (Table VI) for this region for the seven months preceding harvest and the plotted monthly mean departure from normal (fig. 1) show that the precipitation in all the States except Kansas and Missouri averaged slightly above normal in 1903 (*A*), was below normal in 1904 (*B*), and was again above normal in 1905 (*C*). In considering the three months before and during the

heading of the grain, that is, the main growing period, it is seen that in 1903 the monthly precipitation was above normal in all the States with the exception of North Dakota, averaging 0.68 inch above (*D*); in 1904 the monthly precipitation was above normal in only three States, Kansas, Missouri, and North Dakota, being below normal in all the others, averaging slightly above normal for the district (*E*); and in 1905 the monthly precipitation was above normal in all the States with the exception of Missouri, averaging 1.29 inches above normal (*F*). In considering the month during which the grain in the different States heads out, it is seen that in 1903 the precipitation was below normal in Texas, Nebraska, Iowa, and North Dakota, and above normal in the other States, averaging 0.78 inch above for the district (*G*). In 1904 precipitation was above normal in some States and below normal in others, averaging about normal for the district (*H*). In 1905 precipitation was generally excessive over the whole region, with the exception of Wisconsin, averaging 1.05 inches above for the States collectively (*I*).

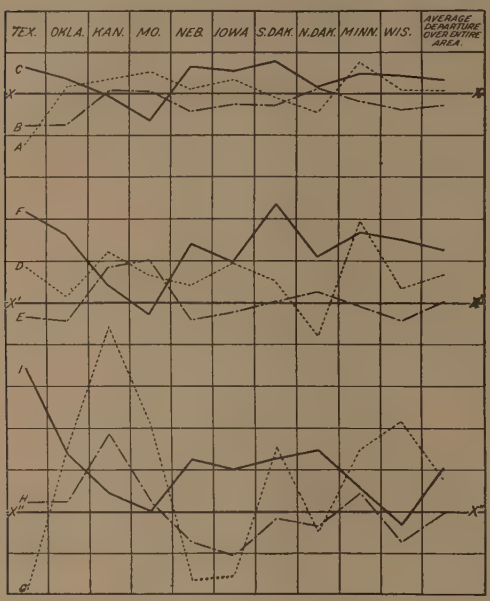


FIG. 1.—Precipitation chart, showing average monthly departure from normal in several States in 1903, 1904, and 1905. *X*, Normal line for a 7-month period preceding the maturity of the grain; *X'*, normal line for a 3-month period preceding the maturity of the grain; *X''*, normal line for 1 month including the heading period; *A*, *D*, and *G*, lines for 1903; *B*, *E*, and *H*, for 1904; and *C*, *F*, and *I*, for 1905. The lines show departure of precipitation from normal during the periods indicated, respectively, the distance between two adjacent horizontal lines representing 1 inch of rainfall.

In considering the precipitation record for the three years, whether for the seven months preceding harvest, for the 3-month growing period in each State, or for the month in which the heading period occurs in each State, it is found that the year 1905 was wetter than either of the other two. If rust depends wholly on the amount of precipitation, whether in a 7-month period, 3-month growing period, or 1-month heading period, the year 1905 should have had more

rust than either 1903 or 1904, while, as a matter of fact, the year 1904 had the most rust.

RELATIVE HUMIDITY.

If the development of rust were in direct proportion to the relative humidity over the whole region, 1905 should have had more than either 1903 or 1904, as the relative humidity during the month containing the critical period averaged about normal in 1903, about 1⅔ per cent above normal in 1904, and approximately 6 per cent above normal in 1905 (78).[1] Of course a certain degree of humidity is necessary for rust development, but an excess over this degree apparently does not increase its virulence.

TEMPERATURE.

Table VII summarizes the temperature records for the several periods in 1903, 1904, and 1905 in the important States of the wheat-growing region.

TABLE VII.—*Temperature record, showing the average monthly departure (in degrees Fahrenheit) from normal in several States in 1903, 1904, and 1905.*

1903.

Month.	Texas.	Oklahoma.	Kansas.	Missouri.	Nebraska.	Iowa.	South Dakota.	North Dakota.	Minnesota.	Wisconsin.	Average.
October	0										
November	+ 4.9	+ 5.3	+4.8	+ 7.3							
December	− 1.1	− 2.3	−5.00	− 2.4	−4.6	− 3.5					
January	− .2	+ 1.4	+3.1	+ 1.1	+6.1	+ 3.5	+ 0.8	+ 2.7	+ 1.00	+ 1.8	
February	− 2.7	− 2.1	−2.6	0	−4.7	− .2	− 3.8	− 3.5	− 1.00	+ .8	
March	− 1.5	+ .1	+2.1	+ 4.8	+1.6	+ 6.6	+ 2.9	+ 4.5	+ 4.7	+ 8.6	
April	− 1.8	− 1.3	− .3	+ .4	+ .1	+ .3	0	+ 1.3	− .7	+ .3	
May		− 3.2	− .2	0	−1.2	+ 1.4	− .5	+ 3	+ .9	+ 1.5	
June					−5	− 5.6	− 2.2	− 1.6	− 2.6	− 4.1	
July							− 2	− 1.3	− 2.6	− 1.1	
Departure from normal:											
Accumulative	− 2.4	− 2.1	+1.9	+11.2	−7.7	+ 2.5	− 4.8	+ 2.4	− .30	+ 7.8	+0.85
Average monthly	− .34	− .3	+ .27	+ 1.6	−1.10	+ .35	− .68	+ .34	− .04	+ 1.1	+ .12
Of 3 crop months—											
Accumulative	− 6.0	− 4.4	+1.6	+ 5.2	−6.10	− 3.9	− .47	+ .10	− 4.5	− 3.7	−2.21
Average monthly	− 2.0	− 1.46	+ .5	+ 1.7	−2.03	− 1.3	− 1.56	+ .03	− 1.5	− 1.23	− .73
Of month containing critical period	− 1.8	− 3.2	− .2	0	−5	− 5.6	− 2	− 1.13	− 2.6	− 1.10	−2.26

1904.

October	− 2.3										
November	− .8	− 1.8	−0.1	− 2.0							
December	+ .1	+ .8	+ .1	− 3.0	+1.3	− 3.9					
January	− 1.1	− .9	− .4	− 2.6	+ .1	− 4.2	− 2.5	− 3	− 4.8	− 6.9	
February	+ 5.4	+ 5.6	+2.6	− .2	+1.7	− 4.8	− 5	− 8.8	− 8.3	− 8.8	
March	+ 5.9	+ 5.9	+4.9	+ 2.5	+4.3	+ 2.4	+ 3	+ 6.9	+ .1	− .8	
April	− 1.1	− 2.4	−4.9	− 6.4	−3.7	− 5.2	− 3.6	− 4	− 4.8	− 6	
May		− 1.6	−2.5	− 1.9	− .6	− .8	0	+ .8	− .6	− .4	
June					−2.8	− 2.5	− 2.4	− 1.7	− 1.9	− 2.4	
July							− 3.7	− 3.6	− 3.6	− 3.4	
Departure from normal:											
Accumulative	+ 6.1	+ 5.6	− .30	−13.6	+ .3	−19	−14.2	−13.4	−23.9	−28.7	−8.67
Average monthly	+ .87	+ .8	− .04	− 1.9	+ .04	− 2.7	− 2.02	− 1.91	− 3.42	− 4.1	−1.23
Of 3 crop months—											
Accumulative	+10.2	+ 1.9	−2.5	− 5.8	−3.77	− 8.5	− 6.10	− 4.50	− 6.10	− 6.20	−3.11
Average monthly	+ 3.4	+ .6	− .8	− 1.9	−1.25	− 2.8	− 2.03	− 1.5	− 2.03	− 2.06	−1.03
Of month containing critical period	− 1.1	− 1.6	−2.5	− 1.9	−2.8	− 2.5	− 3.70	− 3.60	− 3.60	− 3.40	−2.67

[1] Accurate detailed records of relative humidity for this region during the years under consideration are not available, and tabulations are therefore omitted.

TABLE VII.—*Temperature record showing the average monthly departure (in degrees Fahrenheit) from normal in several States in 1903, 1904, and 1905*—Continued.

1905.

Month.	Texas.	Oklahoma.	Kansas.	Missouri.	Nebraska.	Iowa.	South Dakota.	North Dakota.	Minnesota.	Wisconsin.	Average.
October	+ 0.9	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
November	+ .3	+ 2.5	+3.8	+ 3.6	.....	.....	.....	.....	.....	.....	.....
December	− .7	− .5	−1.3	+ .3	+0.9	+ 0.5	.....	.....	.....	.....	.....
January	− 3.5	− 7.8	−8.2	− 7.5	−5.7	− 7	− 5.8	− 5.3	− 5.5	− 6.8	.....
February	−10	−10.4	−8.3	− 8.6	−6.8	− 6.8	− 2.9	− 1.4	− 1.9	− 5	.....
March	+ 3.5	+ 5.5	+8.5	+ 7.8	+8.2	+ 9.1	+10.7	+14.5	+ 7.4	+ 4.2	.....
April	− 2	− 2.2	−1.5	− .1	−2.9	− 1.8	− 1.7	− 1	− 1.7	− 1.8	.....
May	.....	+ .2	−1.1	+ .1	−3.4	− 2.1	− 4.4	− 2.8	− 3.5	− 2.9	.....
June	.....	.....	.....	.....	− .5	− .3	− 2.3	− 3.5	− 1.8	− 1.2	.....
July	.....	.....	.....	.....	.....	.....	− 3.5	− 2.7	− 2.3	− 2.1	.....
Departure from normal:											
Accumulative	−11.5	−12.7	−8.6	− 4.4	−9.20	− 8.40	− 9.9	− 2.2	− 9.3	−15.6	−9.18
Average monthly	− 1.64	− 1.81	−1.22	− .62	−1.31	− 1.20	− 1.42	− .31	− 1.32	− 2.22	−1.31
Of 3 crop months—											
Accumulative	− 8.5	+ 3.50	+5.90	+ 7.8	−6.80	− 4.20	−10.2	− 9	− 7.6	− 6.2	−3.53
Average monthly	− 2.83	+ 1.16	+1.96	+ 2.60	−2.26	− 1.40	− 3.4	− 3	− 2.53	− 2.06	−1.17
Of month containing critical period	− 2	+ .20	−1.1	+ .10	− .50	− .30	− 3.5	− 2.7	− 2.3	− 2.1	−1.42

The temperature records (Table VII) for this region for the 7-month period preceding harvest and the plotted monthly mean departure from normal (fig. 2) show that in 1903 the average monthly temperature for the 7-month period varied less than one-half a degree F. from normal in all States except Missouri and Wisconsin, where temperatures were high, and in Nebraska, where temperatures were low, the average for the whole region being 0.12 degree F. above normal (*K*). In 1904 temperatures were subnormal in all States except Texas, Oklahoma, and Nebraska, and strikingly so in Iowa, North Dakota, South Dakota, Minnesota, and Wisconsin, the average for the region being 1.23 degrees below normal (*L*). In 1905 temperatures were again generally subnormal, but not to such an extent over the five last-named States as in 1904, although the general average below normal was slightly greater in 1905 than in 1904 (*M*). In considering the 3-month period before and during the heading of the grain it is seen that in 1903 the average monthly temperatures were subnormal, with the exception of Kansas, Missouri, and North Dakota, averaging 0.73 degree F. below normal (*N*); that these temperatures were more subnormal in 1904 than in 1903, with the exception of Texas and Oklahoma, averaging 1.03 degrees below normal (*O*); that they were again subnormal in 1905, but more irregularly so than in 1904, with a general average slightly greater than that of 1904 (*P*). In considering the month embracing the critical period it is seen that temperatures were subnormal with striking regularity over the entire region in 1904, averaging over 2½ degrees below normal in Nebraska and Iowa, almost 3½ degrees in Wisconsin, and over 3½ degrees in South Dakota, North Dakota, and Minnesota, with a general average of 2.67 degrees below normal (*R*).

The temperatures in 1903 (*Q*) and 1905 (*S*) were also subnormal during the critical period, but with much greater irregularity and not to such an extent as in 1904.

To recapitulate, it is seen that although the general average of temperatures for the whole area for the 7-month and 3-month periods in 1903, 1904, and 1905 were not much different, still in those States where the rust attack was most severe in 1904, namely, North Dakota, South Dakota, Minnesota, Iowa, and Wisconsin, temperatures for the 7-month period averaged generally much lower in 1904 than in 1905, and for the 3-month period averaged about the same as in 1905. During the 1-month period temperatures were consistently subnormal in 1904, averaging 2.67 degrees below normal for the whole region; temperatures were 3½ degrees below normal over South Dakota, North Dakota, Minnesota, and Wisconsin, this average being considerably lower than that of either 1903 or 1905. It is seen, then, that the unusually low temperature over this region was a very important factor, if not the determining factor, for the prevalence of rust in 1904. Low temperatures made the crop as a whole late.

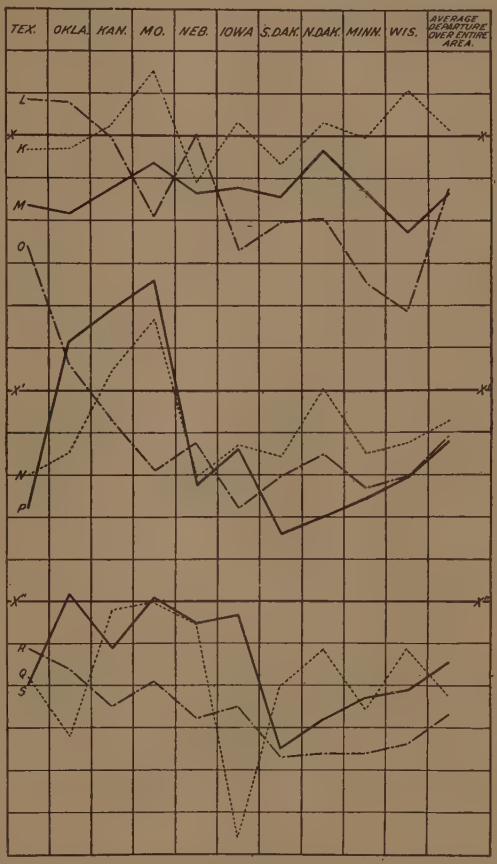


FIG. 2.—Temperature chart, showing average monthly departure from normal in several States in 1903, 1904, and 1905. *X*, Normal line for a 7-month period preceding the maturity of the grain; *X'*, normal line for a 3-month period preceding the maturity of the grain; *X''*, normal line for 1 month including the heading period; *K*, *N*, and *Q*, lines for 1903; *L*, *O*, and *P*, for 1904; and *M*, *P*, and *S*, for 1905. The lines show departure of temperature from normal during the periods indicated, respectively, the distance between two adjacent horizontal lines representing 1 degree F.

Growth was slow and the heading period was delayed and lengthened. The low night temperatures with abundant dews remaining late in the morning were most favorable for spore germination and infection of the growing grain, and a severe rust attack was the result. That rusts were also severe in parts of South Dakota and North Dakota in 1905 was to be expected from the low temperatures that also prevailed during that year in those States throughout the growing and heading period.

PREVENTION OF RUSTS.

In view of the almost universal distribution of rusts, the great variety of rust forms, their complicated life histories and relationships, the ease with which they are distributed, the apparent absence of any weak point in their life history, and the great influence of climatological conditions upon their development, it would seem that there is but little chance to control these fungi or to prevent losses caused by them from year to year. The worker on rusts from an economic standpoint has kept persistently at it, however, and investigations along many lines have been made, a few of which seem to give some promise of success in the future. Three main lines of experimentation have been pursued. These are (1) experiments in spraying, (2) experiments with soil treatments, and (3) experiments in the selection and breeding of varieties resistant to the disease. A comprehensive survey and treatment of these subjects must be reserved for the future, but a few of the more important points will be mentioned.

SPRAYING EXPERIMENTS.

Some of the first spraying experiments for rust prevention in this country were made by Kellerman and Swingle, in Kansas, in 1891 (61, p. 90). Two varieties of spring wheat, Fife and Bluestem, six varieties of barley, and one variety of oats were used in the experiment. The fungicides employed were flowers of sulphur, potassium sulphid, chlorid of iron, and Bordeaux mixture. Spraying was begun when the plants were 2 to 3 inches high and was repeated every eight days, on an average, for 11 successive times. Rains were unusually abundant during the season. Rust appeared plentifully on the sprayed plats and apparently no beneficial results followed the application of the fungicides. Pammel (82, p. 329) made similar experiments with ammoniacal carbonate of copper and Bordeaux mixture. Three applications were made, but were "entirely useless." Galloway (53, p. 198), in 1891–92, performed spraying experiments at Garrett Park, Md. He used a variety of spraying solutions, among which were Bordeaux mixture, ammoniacal copper carbonate, ferrous ferrocyanid, copper borate, ferric chlorid, ferrous

sulphate, cupric ferrocyanid, cupric hydroxid, potassium sulphid, flowers of sulphur, and sulphosteatite powder. Treatments were given when the plants were 2 to 4 inches high in the fall and continued until May 16—seventeen treatments in all.

In June, in spite of all these treatments, "not a leaf could be found that did not show the fungus." The treatments, furthermore, had no appreciable effect on the yield. Under Galloway's direction, Swingle performed similar experiments in Kansas the same year with Bordeaux mixture, ammoniacal copper carbonate, and potassium sulphid. In his experiments "Bordeaux mixture did to a considerable extent prevent rust, but the other preparations had little or no effect on the disease. In no case did the prevention of rust affect the yield to any appreciable extent." At Rockport, Kans., the same year, Bartholomew practically duplicated the Maryland experiments under Galloway's direction. Bordeaux mixture seemed to have a fairly good effect, and Bartholomew concluded that "while no plat was entirely free from rust it is nevertheless a fact that the ravages were reduced to a minimum on the 10-day plats sprayed with Bordeaux mixture and ammoniacal solution of copper carbonate." In summing up all of these experiments, Galloway concluded "that the spraying treatments did, in some cases at least, diminish the amount of rust and similarly increased the yield of straw and grain." Even with the most improved spraying methods known at that time Galloway believed spraying would be impracticable on a large scale. That there was a possibility of making it practicable in the future was conceded. Hitchcock and Carleton further carried on spraying experiments in Kansas in 1893 and 1894 (58, pp. 4–9). They used a large number of spraying solutions. Some of these, particularly potassium bichromate and ferric chlorid, were somewhat effective in preventing rust, but the investigators found it impossible to cover the foliage sufficiently to make them thoroughly efficient. They concluded that "although the rust can be largely decreased, we can not attain prevention as is done in such diseases as the grape mildew. Furthermore, it is extremely doubtful if spraying of wheat or oats would pay, even if effective."

Since these extensive spraying experiments very little work along this line has been done in the United States, although more or less desultory trials have been made. The trouble at all times in spraying for rust has been the impossibility of getting a spraying solution that will cover all parts of the leaves evenly. The more or less waxy bloom which occurs on the leaves of cereals causes the moisture to drop off very easily, and it is almost impossible with any kind of spraying apparatus to wet both surfaces of the leaves equally well. The areas to be covered are so extensive that the expense of spraying

would be very high. It would seem, however, that with modern machinery and the many and varied formulæ for spraying solutions in existence, interesting results might be obtained with further spraying experiments; particularly would this be true in the case of prevention of stem rust of wheat (*Puccinia graminis*), as we now know the critical period for its attack, namely, the heading time of the grains. It would seem possible to limit spraying operations to this period, particularly in years when it falls in a prolonged cold season, thus concentrating the spraying operations. Even under these conditions there is considerable doubt that spraying would ever be of practical value in preventing rust, but the possibilities justify further experiments.

The literature on spraying experiments for the prevention of rusts in foreign countries is extensive and can not be reviewed in this bulletin for want of space. Within the knowledge of the authors, no such experiments have been successful from an economic standpoint, though a few have shown some promise.

SOIL AND SOIL TREATMENTS.

That an excess of some elements in the plant food may predispose a plant more or less to an attacking disease, or that an excess of some other elements may have the opposite effect, rendering the plant more resistant, has not been firmly established. On the contrary, Ward (100, p. 138) has performed experiments to show that nutrition alone does not make for or against predisposition or immunity on the part of the host or virulence or impotence on the part of the parasite. That cereals will absorb sufficient quantities of any element originally in the soil, or which has been applied as fertilizer, to render them resistant to rust attack is thus problematical. If this were possible it would be a difficult matter to explain just how this resistance is obtained, whether from changed physiology, modified morphology of the host, or from some toxic effect against the fungous parasite. We know, for instance, that excess of certain salts in the soil will change not only the morphology but the physiology of cereals. Harter (54, p. 134) has shown that wheat plants grown in soils made saline by the addition of 0.7 to 1.4 per cent of sodium chlorid "modified their structure by depositing bloom on the leaf surface, by thickening the cuticle, and by reducing the size of the epidermal cells." In other words, the plants assumed xerophytic characters. Physiologically, transpiration was decreased in plants on soil sufficiently saline to cause increase in thickness of the cuticle, and was increased in plants in soil containing soluble salts in proportions too small to affect the measurements of the cuticle. Although, as will be discussed later, Ward has shown that the

morphology of grains has little or no effect upon the resistance, physiological effects, such as described, undoubtedly will influence the general resistance or predisposition of plants to disease in some degree, the extent of which has not yet been determined. Experiments in soil treatments for disease prevention have, however, been made from time to time, a few of which will be cited.

In 1891–92 Galloway (53, p. 208) at Garrett Park, Md., treated the soil with various chemicals, among which were flowers of sulphur, air-slaked lime, ferrous sulphate, Bordeaux mixture, potassium sulphid, ammoniacal copper carbonate, and potassium bichromate in various quantities and proportions. No practical results were apparent, and he concluded that "in no case did these chemicals have any appreciable effect on the prevalence of rust." On the other hand, Petermann (83, p. 15) claims that wheat on land fertilized with superphosphate rusted badly, while wheat under similar conditions, but manured with Martin slag (a commercial fertilizer), remained almost rust free. He was inclined to believe that the silicic acid present in the fertilizer was an effective agent in preventing rust.

Further experiments on the effect of fertilizers on crops, both in the United States and in Europe, have been exceedingly numerous in the last few years, but very little careful attention seems to have been given to their effect on cereal diseases. General observations have been made, however, and it is now well established that where there is an excess of nitrogen in the soil, other things being equal, grains are more severely attacked by rust than crops on soil containing less nitrogen (28, p. 659; 60, p. 245; 76, pp. 72, 73; 95, pp. 263–270). Where barnyard manure has been applied heavily the result is similar, and where grains are grown after a crop of clover, beans, or vetch, rusts may be expected. In fact, it may be generally stated that where soils are rich in nitrogen, producing rank and succulent plant growth, rust attacks will, as a rule, be most severe on account of increased succulence of the plants, increased rankness of growth, delay in drying out after showers and dews, and slight delay in the ripening period. On the other hand, phosphate of lime tends to shorten the ripening period and thus acts as a rust preventive to some extent. Careful observations and experiments along this line in the future should give both interesting and valuable results. Care should be taken, however, to differentiate the results in experiments on fertilizers with relation to rust resistance of cereals. In general, a rust attack is most virulent on a healthy plant. This is particularly true of succulent plants in thick stands. As delay in ripening and other effects may also be produced by fertilizers, their relationship to the rust must be carefully kept in mind. The effect of such

results on the rust attack might easily be erroneously attributed to the action of certain chemical constituents of various fertilizers on the rust itself. It seems probable that this is the case in the above-cited results attributed to nitrogen-bearing fertilizers, viz, that the fertilizer produced a very luxuriant growth on which the rust attack would naturally be virulent.

RESISTANT VARIETIES.

CAUSES OF RESISTANCE.

That some plants are far more resistant to the attacks of parasitic fungi than others of the same genus or species has long been noticed, and that this holds true with respect to grains is well established. Some remarkably rust-resistant wheats, such as the durums and the primitive einkorn wherever grown, Extra Squarehead in Sweden, American Club in England, and Rerrarf and Ward's Prolific in Australia, are well known. Some of these varieties, however, can not be said to be universally rust resistant, as one variety may be resistant to one or more species or biologic forms of rust in one country but will not necessarily hold the same balance toward other forms of rust, or in another country (51, p. 36; 39, pp. 340, 341; 44, p. 249; 43, pp. 141–144; 75, p. 27; 30, pp. 59, 60; 28, pp. 661, 662). Thus, for instance, Squarehead is more resistant toward *Puccinia glumarum* in Sweden than toward *Puccinia triticina*, and Rerrarf, while very resistant in Australia, breaks down completely in North Dakota. Numerous instances of this kind might be cited.

It has not yet been established to what character of the plant this elusive and seemingly erratic resistance is due. From a large number of inoculation experiments with the brown rust of bromes and from detailed histological investigations of the hosts, Ward (98, p. 303) found that there is absolutely no relation between differences in the morphology of the brome varieties expressed in length of hairs, number and size of stomata, thickness of epidermis, etc., and rust resistance. He concluded:

> Resistance to infection of the immune or partially immune species and varieties is not to be referred to observable anatomical or structural peculiarities, but to internal, i. e., intraprotoplasmic properties beyond the reach of the microscope and similar in their nature to those which bring about the essential differences between species and varieties themselves.

In the study of resistant and nonresistant wheats the same author (102, pp. 38, 39) showed that rust spores germinate on both susceptible and resistant varieties and gain entrance to them through stomata, but in the resistant varieties further progress is checked by the rapid deterioration and collapse of host cells around the entering fungus, while in the nonresistant varieties the host cells remain turgid

and healthy for a long time, giving abundant nourishment to the parasite. Marryat (70, pp. 129–137) had similar results in working with two wheats, American Club, a resistant wheat, and Michigan Bronze, a highly susceptible variety. She concluded:

> We are forced to fall back upon the theory that immunity to disease is due in these cases to the production of certain toxins and antitoxins by host or parasite, or both, which are mutually destructive.

Salmon (91, p. 88), working on the barley mildew, was similarly led to believe that disease resistance is due to physiological and not structural peculiarities. Bolley (26, pp. 180–182) is not certain whether disease resistance is due to structural or physiological characters, but believes it to be due to the latter, from having been able to develop resistance in every strain of potatoes, flax, or wheat with which he has worked. He further maintains:

> Under uniform conditions of rust infection, all wheats rise rapidly to a stage of marked resistance to general uredospore infection, whether caused by *Puccinia graminis* or *P. rubigo-vera*, which resistance seems to be characteristic for each variety concerned * * * . The facts point quite clearly to the probable influence of chemical agencies, perhaps toxins, arising from the direct existence of fungous attacks upon the hosts. In my mind there is not the slightest doubt but such attacks originate heritable resistance.

Biffen (16, p. 128), after making numerous hybrids between varieties resistant and susceptible with respect to rusts and studying the first and second generations, concluded that "immunity is independent of any morphological character." Orton (81, p. 457), in analyzing the nature of resistance of varieties, similarly concluded that "resistance is due to a specific protective reaction of the host cell against the parasite." To whatever the resistance may be due in the last analysis, it seems to be a peculiar, delicately balanced condition of the host against specific parasites, a balance which is not maintained in the same way toward any two species or varieties and which may be easily upset by change in environment of the host.

SELECTION AND BREEDING OF RESISTANT VARIETIES.

It has long been known that disease resistance is inheritable to a greater or less degree, and on this basis selection of resistant varieties and strains has been going on for some time. Biffen (15, p. 40; 16, pp. 109–128) has recently brought forth experimental results to prove that resistance and susceptibility of cereals to rust are Mendelian characters and are inherited in Mendelian proportions. He collected a large number of wheat and barley varieties of various degrees of resistance to the three rusts, *Puccinia glumarum*, *P. graminis*, and *P. triticina*, common in England, and then made crosses between resistant and susceptible varieties. The hybridizing was done in 1904, and results of growing these in 1905 and 1906 were reported. With

regard to yellow rust, he found that on crossing susceptible and resistant varieties the offspring was susceptible. Upon self-fertilization of these susceptible individuals, resistant and susceptible descendants were produced in the proportion of one of the former to three of the latter, that is, resistance was recessive to susceptibility, the degree of susceptibility being variable. When the degree of susceptibility differed in the two parents the hybrid resembled the more susceptible parent in that respect. More important still, the relatively resistant forms bred true to these characters in the succeeding generations. Bolley (27, pp. 182, 183), from several years' work in the selection and breeding of flax and wheat resistant to wilt and rust, respectively, came to similar conclusions, and in addition believes that unit characters of resistance may be originated even from a very susceptible variety by gradually subjecting the crop to disease from year to year. He maintains that these characters may later be inheritable.

The authors have been engaged in similar work since 1907, but sufficient results have not yet been obtained to pronounce definitely on the question of the application of Mendelian laws to resistance to rust in these experiments. Detailed results of this work are reserved for future publication.

METHODS USED IN SELECTION AND BREEDING.

From the foregoing it will be seen that there are three methods in use for the development of rust-resistant grains through selection and breeding. (1) A careful testing and selection of pure varieties to determine which are already resistant; (2) selection of the best individuals or bulk selection from some strain or variety from year to year under fairly constant disease conditions in the belief that disease resistance is accumulative; (3) hybridizing of desirable varieties with some variety of known resistance and selecting the resistant plants.

The first method is absolutely necessary before the third can be applied, while the second is possible for any worker along this line at any time.

In breeding for resistance to almost any disease, in order to insure rapid progress, the disease must be present every year in sufficient virulence to affect the crop under trial with more or less severity. Certain diseases, particularly rust, occur in epidemical proportions only at irregular intervals. This not only delays results in nonepidemical years but disturbs them in other ways. To overcome these objections, diseases must be promoted yearly on the breeding grounds in every possible way. In order to do this, special breeding plats are employed If one is working for resistance to flax wilt, the breeding plat must be on flax-sick soil; if for drought resistance, on ground particularly

subject to drought; and for rust resistance, on ground where a rust epidemic can be insured. In the case of rust these conditions can be promoted in several ways: (1) By keeping the breeding plats on fairly low ground, where moisture is plentiful but not excessive and where dews remain as long as possible; (2) by planting barberries around or through the plats when breeding for resistance to *Puccinia graminis*, or by planting buckthorns when breeding for resistance to *P. coronata;* (3) by planting winter grains at intervals through the plat where spring grains are being bred (since the rusts, as a rule, occur earlier on the winter than on the spring grains); (4) and most important, by collecting æcidio or uredospores in water and spraying on the plants with hand or knapsack sprayers during the evenings at the period when the grains are most susceptible. All of these methods, or modifications of them, are now in use by Bolley (25, p. 48; 27, pp. 177–182), in North Dakota; by Biffen, in England (16, p. 112), at the Cawnpore Agricultural Experiment Station, in India (55, pp. 54–57); and have been employed since 1907 by the Office of Grain Investigations in cooperation with the Minnesota Agricultural Experiment Station. In Minnesota the authors have established a plat where a very virulent rust attack was obtained, even in the season of 1909, in which no stem rust appeared in any of the fields in its vicinity and in which only local infections were reported throughout the spring-wheat States.

Breeding of this kind is extremely important and should be carried on by agronomists and plant pathologists at every experiment station where conditions are such that rust epidemics may occur at any time. To be effective, it must be extensive and must be persistently employed.

SUMMARY.

(1) Rusts are among the most serious diseases of grains in the United States, causing an estimated annual loss of fifteen to twenty million dollars. In 1904, in the three States, Minnesota, North Dakota, and South Dakota, the loss due to rusts, conservatively estimated, was as high as $10,000,000.

This paper deals only with the rusts of the small-grain crops, wheat, rye, oats, and barley, including *Puccinia graminis*, *P. rubigo-vera tritici*, *P. rubigo-vera secalis*, *P. coronata*, and *P. simplex*.

(2) Practically all these rusts are coextensive with their hosts in the United States, but are not serious in all localities. In general, the areas most affected are the valley of the Mississippi and its tributaries and certain coastal areas. In some years even the drier areas may be affected.

The stem rust of wheat is of great importance in the hard winter and the hard spring wheat belts, is frequent in Washington and Oregon,

is almost always virulent on the coast of California, and is severe and frequent in the southern half of Texas. The epidemic of 1904 was prevalent throughout the entire Mississippi Valley, extended into the wheat fields of the Canadian Northwest, and even invaded the dry lands.

Leaf rust of wheat is also coextensive with the wheat crop and is more common in many districts than stem rust. It occurs yearly over the eastern half of the United States. The losses caused by it are not comparable to those caused by stem rust.

Stem and leaf rusts of oats are coextensive with the oat crop. They usually occur together and are abundant east of the dry belt of the Great Plains region, are paramount in importance in the Southern States, and extend north to the Canadian border and even beyond.

Stem rust of barley is practically coextensive with barley, but is not often present in sufficient quantity to do serious damage.

Leaf rust of barley seems to be of recent introduction. It is economically one of the least important of the grain rusts.

Stem rust of rye is probably widely distributed in small quantities and is fairly common, but causes little injury.

Leaf rust of rye is widely distributed and very abundant, but causes little damage, as the rust is closely confined to the leaves and the rye matures too early to be appreciably damaged.

(3) Botanical characteristics, life histories, and physiological specializations of parasitic fungi may vary with the geographical distribution. European and American forms may be apparently identical morphologically, but are not necessarily identical in their life histories or physiological specialization.

That stem rusts on wheat, rye, oats, and barley, both in Europe and America, may produce their æcidia on barberry has been proved, but that they always do so and can not live for more than one season without passing on to barberry is disproved by experiment.

The æcidial stage of leaf rust of wheat is not known either in Europe or in this country. The uredo stage exists through the winter months, and the rust may live independent of an æcidial stage.

The æcidial stage of the crown rust of oats occurs in Europe on *Rhamnus frangula* L. and *R. cathartica* L. and in the United States on *R. lanceolata* Pursh., *R. caroliniana* Walt., and *R. cathartica*.

The æcidial stage of the leaf rust on rye occurs in Europe on *Anchusa officinalis* L. and *Lycopsis arvensis* L. It is believed that the European and American forms are identical.

The æcidial stage of the leaf rust on barley is not known for Europe or America. This rust seems not to have been previously reported in this country.

Rusts exhibit great variety in regard to complexity of life histories; some are confined to a single host species, some range over two or

more species of one host genus, while others range over two or more genera and often on different tribes of the same family. What appear to be the same forms macroscopically and microscopically are often physiologically different, and may consist of a large number of strains or varieties conveniently called biologic forms. This fact accounts, to a large extent, for the differences in results obtained by American and European investigators working on what are apparently the same species.

In an attempt to break down the barriers between biologic forms the writers have been able to transfer rusts in the uredo stage as follows: Stem rust of wheat (*Puccinia graminis tritici*) from wheat to wheat, rye, and barley, but not to oats; from wheat to barley and then to wheat and rye; and from wheat to barley successively three times and then to oats. Stem rust of barley (*P. graminis hordei*) from barley to barley, oats, rye, and wheat; from barley to wheat and then to barley, wheat, oats, and rye; and from barley to rye, to barley, and then to wheat, oats, and rye. Stem rust of rye (*P. graminis secalis*) from rye to rye and barley; from rye to barley and then to barley, oats, and rye; and from rye successively to barley, to barley, and to rye. Stem rust of oats (*P. graminis avenae*) from oats to oats and barley, but not to wheat or rye. Leaf rust of wheat (*P. rubigo-vera tritici*) from wheat to wheat, rye, and barley. Leaf rust of barley (*P. simplex*) from barley to barley only. Leaf rust of rye (*P. rubigo-vera secalis*) from rye to rye only. Leaf rust of oats (*P. coronata*) from oats to oats and barley, but not to wheat or rye.

There is a measurable difference in size between the uredospores of the stem rust on wheat and the stem rust on barley. In continuous culture experiments of wheat stem rust on barley and barley stem rust on wheat, the uredospore of the wheat stem rust approached the uredospore of the barley stem rust in size and the barley stem rust approached the wheat stem rust in size.

The following points in regard to biologic forms of rusts of cereals may be emphasized: (1) The stem rusts on wheat, barley, rye, and oats are undoubtedly biologic forms of the same species, *Puccinia graminis* Pers.; (2) these forms are not entirely confined to their hosts, but vary in range in part according to the host plants they have been recently inhabiting; (3) the leaf rusts on wheat and rye are more highly specialized than the corresponding stem rusts; (4) the stem rust on barley has ordinarily the widest, while the leaf rusts on barley and rye have the most restricted range; (5) under favorable conditions all the stem rusts can be carried successfully to the four cereals; (6) when rusts are transferred to uncongenial hosts, if pustules are produced they are small and weak; (7) two biologic forms may inhabit the same cereals without being identical; (8) by gradual variation

and adaptation to varying conditions a rust species widely distributed may form a number of strains or types, differing in physiological reactions; (9) the host plants exercise a strong influence not only on the physiological and biological relationships but in some cases even on the morphology of the uredospore.

(4) Rust life histories were very incompletely understood up to 1864–65, when De Bary demonstrated the heterœcism of *Puccinia graminis* Pers., but numerous citations in literature show that barberries in proximity to grainfields had long been believed harmful. From 1865 life-history work on the Uredineæ has made rapid strides and the relationships of many European and American forms of rusts, particularly those of *P. graminis*, have been demonstrated.

Whether or not the æcidium is an essential stage in the life history of rusts has long been questioned. Many authors believe it serves to reinvigorate the fungus, and this view has been strengthened since the recent discoveries of cell fusions and the origin of the binucleated condition in the æcidium of various rust species.

To test this invigoration theory continuous culture experiments from the uredospore of six different grain rusts were undertaken by the writers and 52 successive uredo generations of each rust grown without the intervention of any other spore form. At the end of these experiments cultures were as easily made and the rusts grew as luxuriantly as at the first inoculation. For this length of time, at least, there is no need for a sexual generation.

(5) Whether or not rusts live over winter in the uredo stage has been a mooted question. Investigators in Germany, Denmark, Sweden, England, and the United States have investigated this problem for different rusts with various results. In the United States it has been demonstrated by several investigators that forms of *Puccinia graminis* and *P. rubigo-vera* live over winter in the uredo stage. These results have been reenforced by experiments cited in this bulletin, and the possibility of wintering of the uredo of several rusts in the northern latitudes of the United States has been shown.

(6) Rusts in the uredo or æcidial stages are present in different parts of the country at all times. Like dust particles, which have been proved to be carried hundreds of miles by air currents, these rust spores may be carried from regions where they are plentiful to regions where grain is in a receptive condition.

That large quantities of rust spores are present in the air at various times has been proved by various investigators and by the writers.

(7) A severe rust epidemic was prevalent in the important wheat States of the Mississippi Valley in 1904. In an analysis of the climatological conditions of this region for the years 1903, 1904, and 1905, during the critical or heading period of the grain and during

the 3-month and 7-month periods preceding harvest, it is seen that 1905 had more precipitation than 1903 or 1904; the relative humidity was greater in 1905, but the average temperature, though about the same for the 7-month and 3-month periods during the 3 years, averaged 2.67 degrees subnormal over the whole area in 1904 during the month containing the critical period. It was 3½ degrees below normal in South Dakota, North Dakota, Minnesota, and Wisconsin, the region most affected by rust in 1904. This average was considerably lower than that of the same period in 1903 and 1905 over the same area. It is believed that this unusually low temperature in 1904 was a very important factor, if not the determining factor, for the rust epidemic of that year.

(8) Spraying experiments for the prevention of rusts have been tried from time to time by various investigators, but for the most part without satisfactory results. There is doubt that spraying will ever be of practical value for rust prevention, but as the critical period for wheat, with regard to the attack of stem rust, is now known, further spraying experiments limited to this period may give valuable results.

That excess of some elements in the plant food may predispose a plant to disease or render it more resistant has not been firmly established. That indirectly it will have some influence, by affecting either the physiology or the general growth of the host plant, is very probable.

Where soils are rich in nitrogen, other conditions being equal, rust attacks are, as a rule, most prevalent.

Experiments in soil treatments for disease prevention have been made by various investigators, but no very practical results have been reported. This field of work is promising and should be further investigated.

Some plants are more resistant to attacks of parasitic fungi than others, and it has not yet been definitely established to what character in the plant this resistance is due; but most authorities agree that resistance is due, as a rule, not to morphological but to physiological characteristics.

Disease resistance is inheritable to a greater or less degree, and Biffen has brought forth experimental results to show that resistance and susceptibility of cereals to rust are Mendelian characters. Other investigators have reached similar conclusions.

There are three methods in use for developing rust-resistant grains through selection and breeding: (1) Testing and selection of pure varieties to determine which are resistant; (2) selection of the best individuals, or bulk selection from some strain or variety from year to year under fairly constant disease conditions; (3) hybridizing of

desirable varieties with some variety of known resistance, and selecting the resistant plants.

In breeding for resistance to disease, the disease must be present every year. Rust occurs in epidemical proportions only at irregular intervals, and, therefore, in order to breed for resistance to rust special breeding plats must be employed, where the disease can be produced yearly by conditions particularly favoring its propagation. Wherever efficient breeding of rust-resistant cereals is to be done, such a breeding plat is absolutely necessary.

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